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Breeding, agronomic and morphological examination of lodging in spring wheat (*Triticum aestivum* L.)

by

Alana Jane Kelbert

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

Plant Science

Department of Agricultural, Food and Nutritional Science

Edmonton, Alberta

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Date approved: Sept 5/2003

Abstract

Increasing genetic lodging resistance in Canadian hard red spring wheat (*Triticum aestivum* L.) is an important breeding objective. We conducted a 3-yr study to determine an effective method to screen for lodging susceptibility within a wide range of spring wheat germplasm (25 genotypes), and to determine the effect of lodging on grain yield and quality. Our results suggest that artificially inducing lodging at early milk growth stage is an effective screen for identifying lodging tolerant and susceptible genotypes. Tolerance to artificially induced lodging was mainly found within semidwarf genotypes and susceptibility was found mainly within Canadian bread wheat genotypes. Lodging resulted in reductions of 2 kernels spike^{-1}, 4 mg kernel^{-1}, 3 kg hL^{-1} in test weight and 1.28 t ha^{-1} in grain yield, when averaged over 25 genotypes. Germplasm was identified with increased genetic lodging tolerance. The presence of short, wide basal internodes and thick culm walls was found in some, but not all lodging tolerant genotypes. Short stature is highly correlated with lodging tolerance and is a highly heritable trait for selection within western Canadian wheat breeding programs.

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1.0 Lodging in wheat: A review of literature

1.1 Introduction

One may find a portion of a given cereal crop lying over in the field, particularly under ideal growing conditions. Cultivars unable to support the weight of developing spikes tend to topple over in adverse weather conditions such as high winds, rainstorms and/or hail. This permanent displacement of stems from their upright position is referred to as lodging (Pinthus 1973).

The prevalence of lodging is typically not uniform within a field, and severity depends on the degree to which the culms lean from the perpendicular and the percentage of the field that is lodged. While quantifying the weather conditions necessary to cause lodging, Easson et al. (1993) observed lodging to occur gradually over a period of hours when oscillating plants first fail to return to the vertical and then lay further and further from their vertical position. Harvesting such crops is difficult, yields are often lowered and grain may be of lower quality with reduced market value.

Lodging can occur from a structural failure in the culm or roots, largely depending on environmental conditions and genotype. Stem lodging has traditionally been a trait associated with tall genotypes. Plants held tightly by their roots will bend at the base of the plant. When culms lack moisture and turgidity at plant maturity, they may buckle or break. A culm damaged culm by insects or disease, and/or an inherently weak culm, may topple over when an external force is applied. Using a wind tunnel, Bauer (1964) determined wind velocities of 54-108 km/hr caused stem lodging in German grown wheat. Wind gusts of these speeds occur on the Canadian prairies.

Root lodging appears to be common in short, often semidwarf cultivars that are grown under high moisture conditions. In addition to increased harvest index, modern, semidwarf cultivars have smaller root:shoot ratios than older cultivars (Siddique et al. 1990). Under irrigation or abundant rainfall the root system can become weakly anchored, losing vertical position to an external force. Easson et al. (1993) reported the occurrence of root lodging was more closely associated with the length of a rainfall, than with the total precipitation over a 24h period or high wind speeds.

While studying the relationship between lodging resistance and certain culm characters in oats, Jellum (1962) reported both root and stem lodging occurred in two different study years in Illinois. Root lodging was observed the first year, characterized by below normal temperatures and above normal rainfall. In the hot and dry conditions of the second year, stem lodging was observed. Many researchers have reported lodging severity to be extremely variable from year to year, with a complete absence in certain years.

Lodging has long concerned cereal producers and breeders, and much research over the last century has been devoted to the topic. Western Canadian wheat breeders have identified lodging resistance as an important breeding priority over the next several years (Western Grains Research Foundation 1995). A thorough understanding of various factors governing lodging is important when breeding for such a complex trait. The following literature review outlines the importance of wheat, the possible effects lodging can have on crop growth and yield, plant traits associated with lodging, and the environmental and agronomic factors that affect lodging susceptibility. Opportunities exist to prevent lodging, but ultimately the goal is to develop lodging resistant cultivars. Previous methods for selecting of lodging resistant genotypes are described, as the variable nature of lodging (i.e. occurrence and severity) imposes extreme challenges for its study under natural field conditions.

1.2 Wheat (*Triticum aestivum* L.)

1.2.1 Global importance and production

Triticum aestivum L., spring wheat, is an allohexaploid ($2n = 6x = 42$) with an annual lifecycle. It is thought to have originated in northwestern Iran or northeastern Turkey as a result of hybridization between tetraploid wheat, *Triticum dicoccum* L. and diploid *Aegilops tauschii* L., followed by chromosome doubling (McFadden and Sears 1946). From its emergence 10,000 years ago, *T. aestivum* has diversified in terms of adaptation and end-use quality through mutation, hybridization and selection.

Wheat is a C_3 monocot, with an optimum temperature for growth of 25°C. Wheat grows best on well-drained soils, and has a relatively high tolerance to soil salinity and a moderate tolerance to soil acidity. Seventy-five percent of all production areas in the world receive annual precipitation between 375 to 875 mm (Briggle and Curtis 1987). The western Canadian climate

is relatively dry for production (~300 to 500 mm), which may occasionally limit yield, but is excellent for producing high protein, high baking quality grain.

The presence of gluten in wheat flour lends wheat its unique baking properties. The elastic ability of this protein matrix allows for the retention of carbon dioxide gas during fermentation. Dough is leavened to produce good loaf volume and crumb texture. The amount and quality of gluten will determine the overall flour quality milled from any given cultivar (Finney et al. 1987). With the exception of low lysine content, wheat contains most essential amino acids, minerals, vitamins and lipids.

Significant production occurs in approximately 60 countries, concentrated between the latitudes of 30 and 60°N and 27 and 40°S (Briggle and Curtis 1987). Wheat is the most important food grain consumed directly by humans, with global production exceeding that of rice and maize. In 2002, 568 million tonnes of wheat were produced on 210 million hectares of land, yielding an average of 2.7 t ha^{-1} (FAO 2003). Between 1991 and 2000, China was the largest global producer of wheat (including durum), followed by the European Union, India and the United States. Currently, Canada produces 5% of global wheat production (Canadian Wheat Board 2003).

1.2.2 Canadian wheat

In Canada, wheat is the largest grain or oilseed crop in terms of annual production, with a yield average of 2.2 t ha^{-1} over the last 10 years. In 2002, 15.5 million tonnes were produced in Canada on 8.8 million hectares (FAO 2003). This was 9 million tonnes short of the 5-year Canadian average (1997-2001) and was mainly attributed to drought. Other than winter wheat grown in southern Ontario, 97-98% of wheat is grown on the prairies, with 15-20% of that being durum (*Triticum durum* L.). Winter wheat production only accounts for 3-4% of total production due to the severity of western Canadian winter conditions. Wheat produced in Alberta accounts for a third of all grain grown on the prairies. Canada is currently the second largest exporter of wheat in the world, followed by the United States, as only 20% of Canadian production is consumed domestically (Canadian Wheat Board 2003).

With such a strong reliance on the export market, Canada has focused on developing a consistent, uniform supply of grain, while continually adapting to customer quality needs. Over the past century of breeding, significant advances in early maturity, elevated disease resistance, and higher yield have been made without jeopardizing quality. Specifically in hard red spring

wheat (CWRS), maximum yield potential has increased approximately 6-9 kg ha^{-1} yr^{-1} over the last 90 years (McCaig and DePauw 1994).

To meet customer needs, western Canadian wheat is split into 7 grain quality classes[1]. Each wheat class is visually distinct from one another, enabling rapid, low-cost segregation at grain terminals (Canadian Grain Commission 2003). This physical identification system is referred to as kernel visual distinguishability, or KVD. Kernel shape and weight determine each quality class, while other physical attributes such as colour and protein content will determine the grade within each class. Success of this system depends on the development and registration of only those cultivars physically similar to each other within each class.

Strict seed shape and weight requirements constrain rapid improvement of various agronomic traits. At present, KVD is the only means of wheat segregation in Canada. Until another means of segregation can be widely implemented (eg. variety eligibility declarations), any lenience of these requirements may compromise Canada's reputation of consistently delivering uniform, high-quality classes of wheat (Canadian Grain Commission 2003).

1.2.3 Dwarfing genes

With concerns about the world's ability to feed itself, large efforts were made to increase food-grain production in the early 1960s. Global wheat yields more than doubled between 1966 and 1990 (Khush 1999). Such advances were made through the development of Green Revolution 'high-yielding varieties', which were responsive to high soil fertility conditions. Several traits contributed to increased yield potential, with the newly developed 'high

---

[1] Western Canadian wheat classes (Canadian Grain Commission, 2003):

- *Canada Western Red Spring (CWRS)* wheat is a hard wheat with superior milling and baking quality, particularly for bread.
- *Canada Western Amber Durum (CWAD)* wheat that produces a high yield of semolina with excellent pasta and couscous quality.
- *Canada Western Extra Strong (CWES)* wheat is a hard red spring wheat with extra-strong gluten suitable for blending purposes and particularly frozen dough products.
- *Canada Prairie Spring Red (CPSR)* wheat is a medium-strength wheat suitable for the production of various hearth breads, flat breads, noodles and related products.
- *Canada Prairie Spring White (CPSW)* wheat is a medium-strength wheat suitable for the production of various flat breads, noodles, chapatis and related products.
- *Canada Western Red Winter (CWRW)* wheat is a hard wheat suitable for the production of such products as French breads, flat breads, steamed breads, noodles and related products
- *Canada Western Soft White Spring (CWSWS)* wheat is a soft wheat (low protein) for the production of cookies, cakes, crackers and pastry as well as soup thickeners.

yielding varieties' exhibiting 2-3 times the yield potential of previously available cultivars or landraces (Khush 1999).

Height was reduced through the incorporation of dwarfing genes and this was one of the most important traits contributing to increased yield potential. A shorter plant, particularly during stem elongation, requires less assimilates thereby reducing competition from other sinks. Harvest index is increased, with more assimilates diverted into the production of grain rather than straw (Austin et al. 1980). With less source limitations, the growth and development potential of each yield component may increase. Many experiments report dwarfing genes exert the beneficial pleiotropic effect of improved spikelet fertility, increasing the kernel number spike^{-1}, further enhancing yield potential (Gale and Youssefian 1985).

This reduction in height has dramatically improved the level of lodging resistance found throughout the world. Many researchers are now reporting semidwarf cultivars as the most lodging tolerant lines found within experiments (Stanca et al. 1979; Briggs 1990; Stapper and Fischer 1990; Jedel and Helm 1991). However, not all semidwarf wheat genotypes are lodging resistant (i.e. Canadian winter wheat CDC Kestrel) (D. Salmon, personal communication). Nevertheless, the improvement in lodging resistance from reduced plant height has allowed for high yielding agronomic practices, such as elevated nitrogen levels, to be used without the fear of elevated incidence of lodging. Along with increased kernel number spike^{-1}, unprecedented yield increases of 40% occurred within 10 years of the first semidwarf cultivar release (Gale and Youssefian 1985).

Presently 21 height reducing (*Rht*) genes of major effect have been described, and are classified into two groups: (1) gibberellic acid (GA) insensitive dwarfing genes and (2) GA responsive dwarfing genes (McIntosh et al. 1998). Most of these 21 genes were derived through mutagenesis and are probably of no breeding potential, as their extreme height reductions result in extreme yield reductions. Thus, only a few major height reducing genes are used in commercial breeding programs.

Two of the most commercially important dwarfing genes originated from Japanese cultivars Shirodaruma (*Rht*1) and Akadaruma (*Rht*2), and were incorporated into world wheat breeding programs through the cultivar Norin 10. These GA insensitive dwarfing genes are easily detected in a segregating population, as semidwarf seedlings do not respond to an exogenous application of low concentrations of GA solution (Gale and Gregory 1977). In an experimental analysis of various *Rht1* and *Rht2* isogenic lines in European wheat, Flintham et al.

(1997) reported an average 18% height reduction from GA insensitive genes, along with a large pleiotropic effect on improved spikelet fertility. Although grain size was reduced, the increased number of grains produced an overall yield increase of approximately 15% (Flintham et al. 1997).

The most commercially important GA responsive dwarfing gene, *Rht8*, originated from the Japanese landrace Akakomugi and was introduced into breeding programs by the Italian breeder, Stampelli (Gale and Youssefian 1985). Field trials conducted in the UK, Germany, and Yugoslavia indicate that *Rht8* reduced height 8 cm, on average, with minimal pleiotropic effects on other agronomic characters. Dwarfing genes are now found in the majority of the world wheat germplasm. In the UK and France, for example, 95% of the wheat acreage is sown to semi-dwarf cultivars (Worland and Snape 2001).

In Canada, however, all bread wheat cultivars (with the exception of AC Abbey and AC Superb) do not contain dwarfing genes within their genome. Although attempts continue, the high yield obtained from the incorporation of dwarfing genes has, to date, resulted in low protein levels unacceptable for Canadian standards (Western Grains Research Foundation 1995). In addition, the resulting change in plant architecture may position the spike relatively low to the ground, exposing the grain to a new microclimate. The potential for disease infection may be increased from higher humidity levels (R. DePauw, personal communication). With low levels of genetic resistance to such diseases as fusarium head blight in Canadian wheat cutlivars (caused by *Fusarium graminearum),* one must take all precautions to avoid the potential of infection and prevent severe losses in both grain yield and quality.

1.3 Effects of lodging on crop growth and yield

1.3.1 Yield and yield components

To accurately quantify the effect lodging has on yield, numerous experiments have used artificial lodging and/or lodging-protection treatments in various cereal crops (Table 1.1). Grain yield reductions almost always accompany lodging, with the magnitude of loss dependent on the cultivar, growth stage and severity of lodging (Stapper and Fischer 1987; Jedel and Helm 1991).

Table 1.1. Reduction in yield (%) from artificially induced lodging at various growth stages in cereal crops.

			Yield Reduction (%) Crop stage of lodging application:				
Crop	Reference	Constraint from vertical (degrees)	Heading	Anthesis	Milk	Dough	Pre-harvest
Barley	Sisler and Olson (1951)	90	65	59	48	-	-
		45	27	17	12	-	-
	Day (1957)	90	46	55	38	-	-
		45	13	11	9	-	-
	Briggs (1990)	90	-	21	16	11	6
Oats	Pendleton (1954)	90	-	37	-	17	-
		45	-	14	-	3	-
Wheat	Laude & Pauli (1956)	90	27	35	24	-	-
	Weibel & Pendleton (1964)	90	31	25	20	12	-

The most detrimental effects occur when lodging is induced at heading, or those growth stages immediately following heading. Lodging during this time period will affect both kernel number spike^{-1} and kernel weight, whereas a later induction of lodging (i.e. soft dough to maturity) primarily affects kernel weight (Laude and Pauli 1956; Weibel and Pendleton 1964; Day 1957; Briggs 1990).

Increasing the severity of lodging also increases yield loss. Under artificial lodging protocols (Section 1.7.1) that restrict the crop from recovering, further yield losses may occur. While investigating varietal responses in spring barley to artificial lodging, Stanca et al. (1979) reported permanent lodging at anthesis reduced yield 2.3 t/ha (38%), whereas temporary lodging reduced yield 1.5 t/ha (25%). Permanent lodging 20 days after anthesis reduced yield 1.3 t/ha (22%), whereas temporary lodging reduced yield 0.8 t/ha (14%). Easson et al. (1993) reported that for each 10% increase in lodging severity, spikes had 5 fewer kernels and kernels weighed 2 mg less, resulting in an overall yield reduction of 1 t ha^{-1} of grain.

1.3.2 Grain quality

Grain quality deteriorates when plants lodge. Grain shrivelling may occur, resulting in reduced test weight, reducing flour yield. Pumphrey and Rubenthaler (1983) studied the effect of lodging on soft white wheat under intensive crop management (ICM), and reported test weight from lodged grain was 3-10 kg hL^{-1} lower than that of standing grain. Reductions in test weight are also proportional to the severity and growth stage at which lodging occured. Severe lodging

(Day 1957) or its occurrence at milk stage (Laude and Pauli 1956; Weibel and Pendleton 1964) significantly lowered test weight in barley and wheat samples, respectively.

Lodging can increase the percent protein of grain, with absolute values dependent upon the severity of lodging (Sisler and Olson 1951) and the growth stage of the lodging event (Laude and Pauli 1956; Weibel and Pendleton 1964). In addition, Pumphrey and Rubenthaler (1983) reported grain from naturally lodged wheat had consistently lower milling scores, with decreased feeding rates into the mill, lower flour yield, with a higher ash content and a greater water absorption. The diameter of cookies baked from grain of lodged wheat was consistently smaller than cookies baked from grain of standing wheat (Pumphrey and Rubenthaler 1983).

1.3.3 Physiological effects

Dry matter production is dependent upon the interception of solar radiation (Chhina and Kler 1997). The canopy structure in a lodged crop is far from optimal, with much foliage shaded by plants leaning or lying on top of them. As a result, the ability to capture photosynthetically active radiation (PAR) is hindered, decreasing photosynthetic capability. While evaluating the adverse effects of lodging on light interception, canopy photosynthesis and yield during grain filling in rice, Setter et al. (1997) reported more than 80% of all light intercepted by the crop was within the top 5 cm of the canopies lodged at 75%, whereas the same amount of light was intercepted within the top 80 cm of the non-lodged canopies. The inability of light to be transmitted through the canopy reduced canopy photosynthesis by 70%, relative to erect canopies, thereby decreasing yield by 38% (Setter et al. 1997).

When assimilate demand cannot be met by current photosynthetic supply, accumulated supplies in the vegetative tissues may be remobilized to support grain fill. While examining the partitioning of dry matter and the deposition and use of stem reserves in a semi-dwarf wheat, Borrell et al. (1989) concluded that post-anthesis stem reserves contributed at least 21% of the final crop yield in a standing crop. Thus, if lodging does occur, it is possible that mobilization of accumulated assimilate reserves may compensate for lost photosynthetic capacity, buffering extreme yield losses. A study of temperate grasses in Oregon revealed reductions in dry matter and water soluble carbohydrates in the leaves and stem components of lodged tall fescue, Italian ryegrass and perennial ryegrass, compared to erect plants, during seed development (Griffith 2000). Reporting a relatively low seed yield depression in lodged tall fescue, Griffith (2000)

suggested that this species has a high compensation potential for translocating reserve assimilates from the leaves and stems to support further seed growth and development.

If severe lodging causes stem damage or breakage, xylem and phloem transport may be hindered or even halted, effecting water and nutrient supply, and assimilate transport (Pauli and Laude 1959). Products required for carbohydrate assimilation are unavailable and remobilization of accumulated assimilate to the sink organs is not possible. In the event of root upheaval, plants may be unable to absorb required assimilates for photosynthesis. Furthermore, secondary tillering can occur in a lodged crop, presumably from a reduction in competition for minerals and carbohydrates by the lodged culms. Although rarely maturing, these tillers will compete with the filling grain for available assimilates (Griffith 2000). Moreover, assimilates may decrease due to increased levels of respiration. Such factors as assimilate remobilization, plant recovery (Section 1.3.4), internode elongation (Section 1.5.1), and damaged stems result in high rates of respiration in the stem, decreasing available assimilate supply (Simmons 1996).

Nitrogen in the grain is derived mainly from organic nitrogen present in vegetative plant parts and remobilized during grain filling (Simmons 1996). Thus, the absolute amount of protein in kernels is scarcely unchanged if lodging occurs following the development of vegetative structures. Pauli and Laude (1959) reported the production of carbohydrates decreased proportionally more than protein production when plants were lodged, causing higher percentages of protein in the grain.

In addition to direct physiological losses, lodging may indirectly cause yield reductions from the inability to mechanically harvest the grain and/or increased level of disease and insect infestations. Lodged crops are extremely difficult to harvest with large combines. Experimental estimates of yield loss (Table 2.1) most likely underestimate such losses, as they do not include losses due to interference with mechanical harvesting. Lodging may delay or result in uneven maturity, particularly if secondary tillers develop, increasing the percentage of shrivelled or green kernels. Reduced harvest efficiency, increased drying costs and the presence of volunteers (from unharvestable grain) in the following year cause further losses. Severely lodged cultivars with weak seed dormancy can sprout under moist conditions (Fischer and Stapper 1987) or become susceptible to invasion by soil insects or microorganisms, further reducing grain quality. Increased moisture levels in a lodged canopy can favor the spread of disease, affecting the efficiency of intercepting PAR and/or grain quality. Briggs (1990) reported the incidence of barley scald increased following lodging, but did not affect barley yield or quality. Langseth and

Stabbetorp (1996) reported an increased concentration of more than 65% of the *Fusarium*-induced toxin deoxynivalenol (DON) in lodged plots, compared to nonlodged plots of barley and oats grown in Norway.

1.3.4 Plant recovery

Although yield losses following a lodging event can usually not be avoided, a crop may recover from lodging, as reported by Laude and Pauli (1956) in wheat and Briggs (1990) in barley. Horizontally positioned plants can resume an erect position by the upward bending of upper culm nodes. The portion of the node facing the ground will grow, by cellular enlargement, forcing the upper portions vertical. The pulvinus, an organ located just beneath the solid node plate, is responsible for such growth. It retains the potential for cell enlargement when the remainder of the leaf sheath is fully developed (Bridges and Wilkins 1973). Lateral transport of growth hormones (including IAA) is not involved in the development of the curvature (Bridges and Wilkins 1973). Rather, starch grains and/or calcium oxalate crystals within the pulvinus parenchyma are thought to act as statoliths (i.e. balancing stones), exhibiting an ability to sense gravity (Lersten 1987). The regained erect position allows for the return of photosynthetic capability. The extent of yield loss is, therefore, dependent upon how rapidly the crop is able to recover. In effect, extremely early lodging during periods of intensive growth may not affect grain yield due to this rapid ability to recover. The ability of a given cultivar to regain a vertical position may prevent uneven maturity, and should ease commercial harvesting.

1.4 Plant characters associated with lodging

Many researchers have investigated the association of various plant characters with lodging, using genotypes that differ in lodging resistance. When evaluating this information, which is often contradictory, Pinthus (1973) noted the following points should be considered: First, the reliability of the assessment of lodging resistance is questionable in light of the strong cultivar × environmental interaction effects on lodging (Section 1.7.1). Moreover, some studies have made lodging assessments based on mechanical properties rather than field assessments. Second, varietal differences in lodging are accompanied by differences in many other characters, which may or may not be correlated with lodging. Third, interaction effects of cultivar × different characters on lodging may carry little relevance when performed on a small number of

cultivars. The association of lodging with plant characters must be based on extensive tests of these characters. Finally, a high correlation between a certain plant character and lodging does not imply a causal relationship.

1.4.1 Plant height

Plant height is positively associated with lodging and many researchers have reported moderate to high Pearson correlation coefficient (r) values between increased lodging and taller plants (Table 1.2). Stapper and Fischer (1990) reported differences in plant height explained more than 80% of the variation in lodging scores for the 7 semidwarf and 1 dwarf wheat genotypes they studied. For each centimeter increase in crop height above 91 cm, lodging severity increased by 3.9% (Stapper and Fischer 1990). However, some researchers have reported that a reduction in height did not significantly reduce the likelihood of lodging (Garber and Olson 1919; Atkins 1938; Mukherjee et al. 1967; Zuber et al. 1999).

Table 1.2. Pearson correlation coefficients (r) between lodging and height for both wheat and barley.

Crop	Reference	r
Barley	Murthy and Rao 1980	0.56
	Stanca et al. 1979	0.63
Wheat	Malkani and Vaidya 1956	0.56
	Pinthus 1967	0.62
	Keller et al. 1999	0.79

1.4.2 Culm characters

The culm of most cereal plants is composed of five to seven nodes, with internodes characterized by a conspicuous separate lumen (hollow pith), which occupies 70 to 80% of the culm volume (Lersten 1987). The length of these internodes is shortest at the base of the culm, increasing considerably towards the top of the plant. In general, the highest and lowest internodes have the smallest diameter. Culm wall thickness and degree of lignification are greatest in lower internodes (Percival 1921).

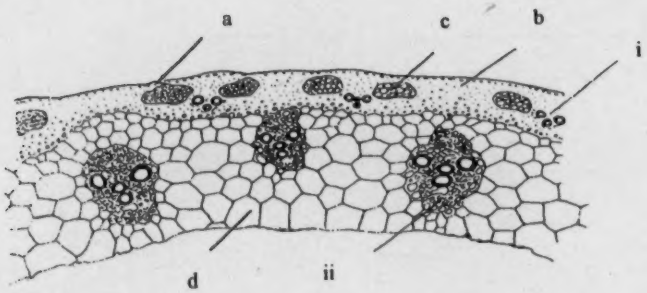

Figure 1.1 Transverse section of a wheat culm, identifying the various anatomical characters (x70).
(Adapted from Percival, 1921, see below for description.)

Anatomically, culm internodes consist of various tissues (Figure 1.1) including:

a) An epidermis.
b) A layer of sclerenchymatous tissue that forms a continuous ring beneath the epidermis, characterized by highly lignified cells.
c) Vertical strips of chlorenchyma (green assimilating parenchyma) embedded within the sclerenchymatous tissue that run parallel along the stem.
d) Large-celled parenchyma extending from the sclerencyhmatous ring to the large central lumen.
e) Vascular bundles, which are either situated in the ring of the sclerenchymatous tissue just beneath the epidermis (i), or within the ground parenchyma (ii). Monocot vascular bundles are closed, surrounded by a bundle sheath of thick-walled lignified sclerenchyma cells, with those found in the ground parenchyma much larger in diameter than those found in the sclerenchymatous tissue.

Numerous studies have reported differences among lodging resistant and susceptible cultivars for various morphological and anatomical plant characters. As stem lodging occurs at the base of the plant, the basal portion of the plant is particularly important. In most studies, samples were taken from the second lowest internode and analyzed for differences in culm characters.

When lodging resistant and susceptible cultivars were compared, significant differences were reported for basal internode lengths (Brady 1934; Atkins 1938; Stanca et al. 1979; Dunn and Briggs 1989). A larger basal culm diameter may also contribute to lodging resistance, with

strong negative relationships reported between lodging and basal culm diameter in wheat (Mukherjee et al. 1967 {r = -0.59}; Zuber et al. 1999 {r = -0.70}) and in oats (Jellum 1962). The diameter of the culm, however, has not always been related to lodging. Many researchers have reported no association between culm diameter and lodging in wheat (Atkins 1938; Malkani and Vaidya 1956; Pinthus 1967) or in barley (Stanca et al. 1979; Dunn and Briggs 1989).

Increased culm wall thickness may enhance lodging resistance. Reports in barley (Dunn and Briggs 1989), wheat (Brady 1934; Mulder 1954) and oats (Jellum 1962) indicate lodging resistant cultivars exhibit thicker culm walls than lodging susceptible cultivars. However, some studies found genotypes (ranging in lodging susceptibility) did not differ in culm wall thickness (Malkani and Vaidya 1956; Pinthus 1967; Stanca et al. 1979; Travis et al. 1996).

In a very early investigation into factors influencing lodging in pre-Green Revolution cereals, Brady (1934) reported the most significant anatomical feature related to lodging resistance was an increased number of vascular bundles. Zuber et al. (1999), however, reported an insignificant correlation between the number of vascular bundles and lodging in wheat. Stanca et al. (1979) and Dunn and Briggs (1989) also found no association between the level of lodging resistance and number of vascular bundles in barley. Jellum (1962) specifically recorded the number of vascular bundles found within the sclerenchyma ring or the inner parenchyma layer in cultivars varying in lodging resistance. No consistent differences among cultivars were found for the total number or location of vascular bundles in the studied oat cultivars (Jellum 1962).

A wide sclerenchyma ring has been associated with lodging resistant cultivars (Brady 1934; Dunn and Briggs 1989). Of the five characters they studied, Garber and Olson (1919) found the thickness of the sclerenchyma ring to be the closest character related to lodging in cereals. Jellum (1962), however, found no consistent differences for the width of sclerenchyma layer in oats. Malkani and Vaidya (1956) found no relation between the width of the sclerenchyma ring and lodging percentages, but they did report the number of cells in the sclerenchyma layer was negatively correlated with lodging in wheat (r = -0.78).

1.4.3 Root characters

Hamilton (1951) reported oat cultivars with a high degree of lodging resistance were generally found to produce large, widely spreading and rigid adventitious roots. Cultivars that lodged easily were found to possess smaller and more flexible roots, which had a greater tendency to grow downward in the soil. Pinthus (1967) reported the angle of root spread in

adventitious wheat roots was related to lodging, with a strong negative correlation (r = -0.70) between spreading angles and lodging score.

Other researchers also reported longer, more rigid adventitious roots (Ennos 1991) with larger spreading angles (Crook and Ennos 1993, 1994) increased lodging resistance in wheat. Malkani and Vaidya (1956), however, reported no relationship between the spread of roots, root weight and volume, and percent lodging in wheat.

1.4.4 Chemical components

The relationship of chemical components to straw strength has long been investigated. Very early work by Sir Humphry Davy associated lodging with low silica (SiO_2) content of straw (Davy 1821). Although Davy's work was based principally on speculation, others have also reported lower silica levels in lodged wheat plants (Phillips et al. 1931; Malkani and Vaidya 1956 {r = -0.61}). Silica is found mainly in the cell walls of the epidermis in wheat, to which it imparts hardness (Percival 1921). Kaur et al. (2001) studied the effect of nitrogen and planting techniques on height, lodging and silica in wheat. They too reported lodging resulted from decreased silica content in stems.

Cellulose and lignin content in basal internodes have been associated with lodging resistance. However, like many of the other characters, results are inconsistent and sometimes contradictory. Mulder (1954) reported low lignin content in lodged wheat plants, whereas Phillips and Davidson (1931) postulated high lignin content creates brittle culms that tend to break under the violent impact of winds. Other studies indicate lignin content did not differ among lodging resistant and lodging susceptible wheat cultivars (Malkani and Vaidya 1956; Travis et al. 1996). Pinthus (1973) suggested that the inconsistent relationships between these characters and lodging resistance reported in the literature may be due to changes in chemical composition during plant development. Stanca et al. (1979), however, found no clear relationship between lodging and lignin, cellulose and hemicellulose content in basal internodes of barley samples taken over a 10-day period.

1.4.5 Other plant traits

The ability of cereals to tiller may also influence the probability of lodging. Pinthus (1973) suggested that high tillering cultivars are less prone to root lodge, due to better-developed root systems. In contrast, Brady (1934) reported high tillering cultivars lodged more due to weak

culms. Others found no significant relationship between tillering and lodging in wheat (Clark and Wilson 1933; Malkani and Vaidya 1956) and oats (Hamilton 1951).

Factors such as maturity date have also been associated with lodging. Atkins (1938) reported a small, but significant positive correlation between lodging and date of maturity in two of the three test years. In a study conducted on Indian wheat, Mukherjee et al. (1967) reported early maturing cultivars were more susceptible to lodging, as unfavorable weather conditions can prevail at the time when proper mechanical tissue development has yet to take place, whereas those cultivars that are late maturing tend to escape those conditions which cause lodging in India. Stapper and Fischer (1990) also reported less lodging in earlier maturing genotypes. The effect of this character on lodging, however, varies with the time of the lodging event.

Other characters including head density and shape may relate to lodging through the effect on the wind resistance (Grafius 1958). The accumulation of raindrops on spike awns may increase the weight of the head and thus increase lodging potential. Pinthus (1967), however, did not report a relationship between lodging and awnedness in wheat.

1.5 The relationship of environmental and agronomic factors with lodging

1.5.1 Light, temperature and moisture conditions

The basal internodes of a wheat plant tend to remain short during development, with little elongation occurring. However, under low intensities of light, elongation of these short basal internodes may occur. Under high light intensities, the action of natural gibberellin (a hormone that promotes both division and elongation of cells) is blocked (Sachs 1965). Consequently, low light intensity promotes etiolated growth, causing internode elongation, thereby decreasing culm diameter and culm wall thickness due to an inverse relationship between the rate of cell elongation and transverse growth (Sachs 1965). A reduction in the quantity and quality of light will reduce carbohydrate assimilation, which may interfere with cell wall development and lignification (Salisbury and Ross 1992).

Some studies have determined that shading on cereal culms may result in a 25% increase in internode length (Holmes et al. 1960; Mulder 1954). Culm diameter and wall thickness of oats were reduced (Mulder 1954) and solidness of the lower internodes of wheat was decreased (Holmes et al. 1960) when subjected to artificial shading. Artificial shading of field plots, which

reduced the light intensity during the boot to heading stage of the 2-4 lowest internodes by 35-75%, promoted severe lodging in wheat (Holmes et al. 1960).

Internode elongation may presumably be affected directly by weather conditions during a given growth period. Mulder (1954) reported that growing conditions during the period of elongation of the lower internodes of the cereal plants are strongly related to lodging tendency. The combination of favourable moisture conditions, relatively high temperature, and excessive nitrogen supply (Section 1.5.2) during this growth period gives rise to a rapidly growing plant, which may increase lodging susceptibility.

1.5.2 Soil fertility

Nitrogen availability is, perhaps, the most commonly cited factor enhancing lodging. Its ability to alter plant morphology can create an extremely lodging susceptible plant. Abundant nitrogen supply increases meristematic activity of a plant, favoring tiller development and survival, as well as increased leaf size and longevity (Hay and Walker 1989). Any increase in crop density decreases the quantity and quality of light transmitted through the canopy, causing etiolation and internode elongation.

Abundant nitrogen supply increases overall plant height (Casserly 1957; White 1991; Crook and Ennos 1995; Kaur et al. 2001). However, the effect on the basal portion of the plant is particularly important to stem lodging. To study the morphological characters related to lodging, Malkani and Vaidya (1956) applied heavy doses of nitrogen to ensure lodging. In so doing, they found the length of the lower internodes increased under high nitrogen management.

Mulder (1954) studied the effect of mineral nutrition on lodging in cereals in the Netherlands. He determined the overall effect of nitrogen on the lower internodes was not direct, but rather the result of shading through increased tillering and leaf formation. Plants with equal nitrogen dressings possessed considerably longer basal internodes with greater crop density due to higher seeding rates or narrow interrow spacings (Mulder 1954). In addition to the indirect effect of shading, nitrogen may directly influence the development of mechanical tissue in the culm. Reports indicate both the sclerenchyma ring thickness and the degree of vascular bundle lignification were reduced under excessive nitrogen management (Mulder 1954; Malkani and Vaidya 1956).

The occurrence of lodging from abundant nitrogen supply is well known and has been documented in various cereal crops around the world (Mulder 1954; Malkani and Vaidya 1956;

Ramanujam 1958; Pinthus 1973; Pearson et al. 1989; Chalmers et al. 1998; Kaur et al. 2001). Early applications promote tillering and extensive elongation of basal culm internodes, increasing the susceptibility of lodging (Gravelle at al. 1988), whereas later applications produce fewer, shorter stems (Chalmers et al. 1998). Split applications may decrease the probably of lodging (Gravelle et al. 1988).

Ayoub et al. (1994), studied nitrogen management on bread quality wheat in eastern Canada and reported a split nitrogen application (60% seeding, 40% heading) reduced the risk of lodging, compared to a one time application at seeding. Chalmers et al. (1998) found mean lodging scores were reduced across study sites by 7% when applications were split (growth stage (GS) 21-24 then GS 30-31, Zadoks et al. 1974) for an oat crop grown in the UK. Such an application scheme may increase yield, not only from a reduction in lodging, but also by providing an adequate nitrogen supply during the critical heading period.

Proper phosphorous and potassium fertility may also enhance straw strength. Phosphorus deficient plants suffer from poorly developed culm walls (Casserly 1957), with reduced sclerenchymatous tissue and fewer vascular bundles (Mulder 1954). Potassium deficient plants have been reported to exhibit reduced culm diameters and culm wall thickness resulting in weaker overall culms (Mulder 1954). However, other researchers have reported that phosphorus and/or potassium are not associated with lodging (Chapman and Mason 1969).

1.5.3 Seeding rate and depth

Numerous studies indicate lodging may be prevented or reduced by decreasing plant density through a reduced seeding rate (Stapper and Fischer 1990; Easson et al. 1993). Up to a certain plant density, cereal plants can compensate for reduced stands through increased tillering (Power and Alessi 1978) and higher kernel number spike^{-1} and kernel weight (Hay and Walker 1989). Easson (1992) determined winter wheat (but not spring wheat) grown in the UK, lodged less following a reduced seeding rate, and yield remained constant.

As seeding rate increases, straw may become weaker (Sisler and Olson 1951) and thinner (Hamilton 1951), with a lower culm density at basal internodes (Mulder 1954). Jellum (1962) determined stem diameter, number of vascular bundles, culm wall width, pith cavity diameter, and sclerenchyma layer width all decreased as the seeding rate increased, although varietal response was not uniform. Easson et al. (1993) reported plants had stronger stems (wide stem

bases with thick walls) with an increased number of adventitious roots under low seeding rates in winter wheat.

Narrowing interrow spacing, while maintaining a desirable seed rate, reduces plant competition and thus the effect of shading. The use of narrow row spacing has been reported to reduce the length and increase the diameter and wall thickness of basal culm internodes of wheat (Watson and French 1971). Reports indicate lodging decreased in wheat (Humphries and Bond 1969; Roth et al. 1984) with an increase in straw strength (Sisler and Olson 1951) under row spacing less than 25 cm. However, Clark (1976) found no improvement in lodging resistance in oats, barley and/or wheat by altering row spacing (53.3 cm vs. 17.8 cm) in southern Ontario.

Johnston and Stevenson (2001) studied seeding rate and seed placement on the yield of hard red spring wheat in Saskatchewan. Lodging increased with an increased seeding rate in row seeding (23 to 30 cm spacing), but air seeding reduced the incidence of lodging at higher seeding rates. The ability of air seeding equipment to randomly spread seed increases the distance between plants, thereby reducing inter-plant competition. Although Johnston and Stevenson (2001) did not find an increase in yield from a crop grown with sweeps, lodging was reduced from the dispersed plant pattern compared with distinct rows. They attributed an improvement in light transmission to the decreased incidence of lodging.

Sowing depth may alter lodging resistance. Ramanujam (1958) suggested deeper sowing might increase lodging resistance, positioning the root crown deeper in the soil. Anchorage of the plant may be strengthened, while germination may be reduced, thereby preventing a thick stand. Hamilton (1951) however reported that deeper seeding tended to promote poor root anchorage. Roth et al. (1984) reported seeding at shallow depths increased lodging in soft red winter wheat grown in Pennsylvania.

In western Canada there is a narrow window for seeding, but in regions where there is more flexibility in planting dates, opportunity may lie in adjusting the seeding date to reduce the probability of lodging. Stapper and Fischer (1990) reported less lodging when irrigated wheat was sown later in Australia. One may alter the seeding date to avoid lodging-inducing conditions, such as disease infestations or unfavorable weather conditions. In a photosensitive plant, seeding date can affect the degree of tillering and the period in which stem elongation will occur. Later sown plants are exposed to longer day lengths and are therefore forced to reach spike emergence earlier, restricting the amount of tillering and internode elongation (Salisbury

and Ross 1992). In terms of root development, Hamilton (1951) found later planting was associated with poorer root development, especially in lodging resistant cultivars.

1.5.4 Disease and insect influences

Diseases and insects that infect the culm and root system can weaken plants and promote lodging. Disease epidemics have the potential to cause widespread lodging, while insect-induced lodging mainly affects individual culms distributed within a field. Most diseases and insects that could potentially cause lodging are not of significance in western Canadian production systems.

Cephalosporium gramanium (eyespot), caused by *Pseudocerosporella herpotrichoide,* may promote stem lodging, particularly in wheat (Mundt 2002). This monocyclic fungus can form brown, elliptical lesions on the lower culm internodes. Deep penetration of these lesions may eventually girdle the culm near ground level, causing stem breakage to occur. Infection is favored by high humidity under a dense crop canopy with high soil moisture. Interestingly, these are conditions already conducive to lodging. Pinthus (1973) indicated it is difficult to decipher the relationship between eyespot and lodging. Although eyespot was prevalent in eastern Canadian winter wheat, proper crop rotations have minimized its presence. Severe infections of take-all (*Gaeumannomyces graminis*), a root-roting disease, may also enhance root lodging in individual plants (Martens et al. 1994).

Pinthus (1973) reported that Hessian fly (*Mayetida destructor* L.) and sawfly (*Cephus cinctus* L.) have potential to cause lodging. The maggots of the Hessian fly girdle culms at the base by scratching the leaf sheaths and internodes, whereas larvae of the sawfly bore within stems. During the late 1930s and early 1940s Canadian wheat crops were severely infested by wheat stem sawfly. Through the development of solid-stemmed cultivars, breeders in Saskatchewan were successful in developing the first sawfly resistant cultivar, Rescue, in North America. This was followed by a succession of improved sawfly resistant cultivars (DePauw et al. 1995). Lodging induced by sawfly infection is presently controlled through genotypic resistance in western Canada.

1.6 Strategies for lodging prevention

As demonstrated above, agronomic practices can be altered to protect yield while diminishing the probability of lodging. Options such as the application of plant growth regulators

or the use of cultivar blends may also be employed to diminish lodging probability under ideal growing conditions.

1.6.1 Plant growth regulators

The application of plant growth regulators (PGRs) is one modern technique that has been successfully employed to reduce lodging in cereals. Although not commonly used in North America, PGRs have been used extensively in the UK, particularly in wheat. With the majority of the UK's cereal production under intensive management, the integration of high plant densities, along with high fertilization create optimal lodging conditions. Since their introduction forty years ago, the use of PGRs has offered some immediate resistance to lodging through a reduction in height, thereby promoting high yield potential.

Chlormequat chloride (2-chloroethyl thrimethyl ammonium chloride) and ethephon (2-chloroethylphosphonic acid) are the two most commonly used PGRs in cereal production. Both exhibit a tendency to reduce height (Cox and Otis 1989; Khan and Spilde 1992), but differ in their modes of action. Excluding ethephon, all PGRs used as anti-lodging agents inhibit gibberellin biosynthesis (a plant hormone responsible for stem extension) at different stages of the biochemical pathway. Ethephon, when absorbed in the cell at neutral or alkaline pH, forms ethylene, a plant hormone known for its ability to inhibit stem elongation (Salisbury and Ross 1992).

Depending on the growth stage of application, PGRs primarily affect either the upper or basal internodes of the plant (Stanca et al. 1979; Dahnous et al. 1982; Pearson et al. 1989; White 1991; Webster and Jackson 1993; Olumekun 1996). The length of basal internodes have been reduced 43% in winter wheat grown in the UK through the application of PGRs (Olumekun 1996), with overall height reductions of up to 31% reported in winter oats (Leitch and Hayes 1990). The ultimate reduction in height depends largely on levels of exogenous nitrogen applied and the cereal genotype.

Reduction in height due to PGR application commonly results in a reduction in lodging (Knapp et al. 1987; Simmons et al. 1988; Khan and Spilde 1992; Easson et al. 1992). Dahnous et al. (1982) reported the complete absence of lodging in all barley and triticale plots after ethephon treatment. Although complete control of lodging is not always obtained, many reports indicate lodging severity is reduced (Stanca et al. 1979; White 1991) or delayed until later stages of grain-fill (Webster and Jackson 1993).

It is the simple reduction in height that appears to confer lodging resistance from the application of PGRs. Inhibiting internode elongation promotes thicker stems, with wider culm diameters and culm walls. Reports indicate lignin, cellulose and/or hemicellulose contents are not altered by the application of either chlormequat chloride or ethephon (Clark and Fedak 1977; Knapp and Harms 1987).

Conflicting results have been reported for yield. The affects of PGRs are dependent on 1) application time in relation to crop growth stage, 2) the presence or absence of lodging, and its time of occurrence and severity, 3) the influence of abiotic stresses 4) the interaction with and effect on partitioning of current photosynthate and/or 5) genotypic differences in response to PGRs (Rajala and Peltonen-Sainio 2000). Consistent increases in yield have been reported when severe lodging was avoided, permitting the crop to benefit from high nitrogen application (Dahnous et al. 1982; Wiersma et al. 1986; Pearson et al. 1989; Khan and Spilde 1992; Easson et al. 1993; Webster and Jackson 1993). However yield reductions have been reported even when lodging is prevented (Knapp and Harms 1988). As well, if more than one application is applied to avoid lodging, yields may decrease as a result of retarded, reduced vegetative growth (Leitch and Hayes 1990) and grain quality may be negatively affected (Knapp and Harms 1988).

Clearly, more research will be needed to ensure lodging resistance is achieved and high yields are maintained with the application of PGRs. Rajala and Peltonen-Sainio (2000) foresee no global increase in the use of PGRs. Dwarfs and semidwarfs cultivars have replaced the tall cultivars that dominated UK production in the 1960 and 70's, and the present emphasis on sustainable agriculture is reducing nitrogen inputs and the use of chemicals. PGRs may have increased importance in North America, offering potential lodging resistance to those areas where breeding programs have not yet been successful in developing lodging resistance cultivars.

1.6.2 Cultivar blends

Another strategy for the reduction of lodging may be through the use of cultivar blends. In theory, a mixture of seed from two or more cultivars will lead to consistently higher yield than the average of each genotype, due to a buffering effect within environments (Poehlman and Sleper 1995). However, cultivars composing the blend must have uniform maturity and be compatible for end-use processing. The proportion of each cultivar may determine the success of the blend (Grafius 1966).

Jackson and Wenning (1997) set out to determine if agronomic performance and end-product quality could be improved by blending two hard red spring wheat cultivars in California, varying in extremes for grain yield and quality, disease susceptibility and lodging resistance. Although no significant differences in yield were found between blends and individual cultivars, this research group reported blends rated better for disease and lodging resistance when compared to individual genotypes. Grain protein and baking quality improved over the lower quality, lodging resistant cultivar. Stutzel and Aufhammer (1989) reported similar results, with a decrease in lodging, but no apparent yield advantage for barley cultivar blends grown in Germany. Grafius (1966) reported an increase in yield stability from a mixture of lodging susceptible and resistant oat cultivars grown in Michigan. Favorable mixtures were found to decrease lodging and improve test weight and yield.

1.7 Breeding for lodging resistance

An improvement in lodging resistance is one feature that can be ascribed to semi-dwarf high-yielding cereal cultivars developed in much of the world over the last 40 years. Elevated lodging resistance has been achieved by reducing plant height and through the selection for high yields under fertile conditions: an indirect selection for lodging resistance.

The development of short-strawed cultivars and the introduction of PGRs have served to improve lodging resistance in cereal grains on a global basis. Breeding for lodging resistance remains a priority in regions of high yield potential. The development of resistant cultivars is the most cost-effective, sustainable, and long-term solution to lodging. However, strong environmental influences complicate the evaluation of lodging resistance. Lodging is very unpredictable and developing an appropriate selection screen for breeding purposes has proven elusive. Whatever the means of selection, it should be reliable, repeatable and efficient.

1.7.1 Selecting for lodging resistance

Direct field assessments

Selection in a plant breeding program is based on assessable variation within breeding lines. In a given year, natural lodging may occur to such a limited extent that no differentiation is possible. In a year where conditions are conducive to lodging, all lines may lodge, again not

enabling one to make a distinction between lines. Because of the ability of cereal grains to recover from lodging, the timing of scoring is important. Underestimation of lodging potential could be made if genotypes are scored only once prior to harvest. Without a proper rating system, it may be difficult to differentiate breeding lines. Given the often random appearance of weather events contributing to lodging, natural lodging assessments in the field may not provide valid information for selection (Atkins 1938). Breeders have therefore developed various indirect selection methods.

Artificial selection techniques

An artificial screen inducing lodging allows for the selection of lodging resistance germplasm, as well as the determination of the ability of a genotype to recover from such a force and its effect on yield. Techniques involving the use of wind to induce lodging have been reported in the literature. Bauer (1964) made use of wind tunnels to evaluate plants grown in pots. Harrington and Waywell (1950) induced lodging by exposing plots individually to strong wind produced by an airplane propeller. Although differences among genotypes were reported, they concluded that this technique was too laborious for practical use.

Laude and Pauli (1956) induced lodging by manually bending and pinching the stems between their fingers. This manual infliction of lodging was done from stem elongation until field maturity. They indicated the wounds appeared similar to those of naturally lodged plants after a storm.

Sisler and Olson (1951) introduced a technique to artificially induce permanent lodging, which was later used by various other researchers in various cereal crops (Pendleton 1954; Day 1957; Day and Dickson 1958; Weibel and Pendleton 1964). A wire mesh was installed in each plot 30-60 cm above the ground, and the crop was allowed to grow up through the mesh. At various growth stages (Table 1.1), varying degrees of lodging were imposed by horizontally moving the wire mesh so that the plants were leaning at a predetermined angle of lodging. Complete lodging was induced by gently forcing the plants over with a board. A wire mesh was placed on top of the plants, securing it so that the plants remained flat on the ground. It was not possible, however, to prevent the stems of the plants from bending at the nodes during subsequent growth. Control plots maintained an erect position by permanent support from wire mesh that was periodically raised as the plants grew. Recently, a similar method was used by Setter et al. (1997) to artificially lodge a rice crop.

Stanca (1979) induced lodging at anthesis and 20 days after anthesis by gently drawing a heavy board over the plot and then pegging down plots with monofilament netting. The plots were either kept lodged for 7 days or permanently until harvest, inflicting varying degrees of severity. Two controls were included, one physically supported by a plastic net frame as done by Sisler and Olson (1951), and the other control left without any physical support. Varying degrees of lodging susceptibly were recorded within that study, with varying effects on yield (Stanca et al. 1979).

The time required in administering such techniques to a large number of lines in a breeding program may be substantial. Although the effect of permanent lodging on yield can be evaluated, data on lodging differentials between lines cannot be collected under permanent lodging conditions, nor can lodging recovery be determined. The application of permanent lodging may not be similar to natural lodging as plants are not allowed to regain a vertical position and yield losses from lodging may be overestimated.

A simple artificial lodging test was proposed by Briggs (1990) to obtain improved data on lodging resistance and recoverability of barley cultivars. Lodging was induced by completely flattening the middle rows of the plot by dragging a plywood board, mounted on 6-cm skids, across the length of each plot, causing a momentary force on the plots. Jedel & Helm (1991) used a similar apparatus, which also progressively pushed down the crop in one direction with minimal stem breakage occurring. With the evaluation of yield losses at various significant growth stages (Jedel & Helm 1991), along with visual lodging scores over time (Briggs 1990), they both determined this technique would be useful for selection of lodging resistant genotypes in a breeding program. Such a technique requires limited resources in terms of equipment, time & skill.

Specific plant traits

The ability to relate specific plant character(s) to lodging resistance may improve selection for lodging resistance. Moreover, selection could be accomplished in early generations, thereby increasing the efficiency of the breeding program. Selection based on short basal internodes, a large culm diameter and thick wall, a high number of vascular bundles, and/or a thick sclerenchyma layer and cell walls may be feasible with modern microscope equipment.

The precision of a correlation is based upon the quality of phenotypic lodging data, the sample size and the degree of stability of a character across environments. To subscribe a given

plant character's contribution to lodging resistance, some researchers have made use of multiple stepwise regression. Zuber et al. (1999) observed that head weight produced an insignificant negative correlation (r = -0.23) with lodging, but the inclusion of the variable in a multiple linear regression model resulted in an increase in R^2. For the 15 genotypes they studied, 77% of the variation in lodging was explained by dry weight per unit length of culm and head weight. A heavier head increased lodging, but was compensated by a heavier stem, which reduced lodging.

With little success in attributing any one plant character to lodging resistance, some researchers have combined several plant characters into lodging indices and/or calculated mechanical straw and root parameters. In theory, this leads to stronger correlations and results in a better selection criterion for lodging resistance. In practice, however, most have proven of little value in breeding programs.

Grafius and Brown (1954) suggested lodging resistance may be assessed by determining straw strength (i.e. the weight that a culm can support) through the calculation of a lodging resistance factor (cL_r). $cL_r = F/b$, where b = culm length (cm), and F = bending force (g), determined at the point where the culm stops downward bending from an attached metal chain of known weight attached to the peduncle. They found this to be effective for the selection of lodging resistant lines of oats, with a repeatability of r = 0.73 and a highly significant correlation coefficient with lodging (r = -0.48). Close correlations between this factor and lodging resistance were also found for barley (Grafius 1958), but no such correlation was found in wheat (Mukherjee et al. 1967). Grafius (1958) found the correlation between the cL_r and lodging resistance in oats was affected by differences in the panicle area.

Conflicting reports on the importance of specific plant characters (Section 1.4) may be attributed to a number of factors. The growth stage at plant sampling may account for variation. Zuber et al. (1999) reported lower correlations with lodging from characters measured at maturity (ZGS 92) than those measured at anthesis (ZGS 65). They attributed this to diminished water content of vegetative parts at maturity compared to anthesis. Jellum (1962) found cL_r values in oats changed in relation to maturity, declining during a 15-day period following anthesis and then levelling off. The strength of an association may be largely dependent upon the degree of lodging in the field. Zuber et al. (1999) reported higher correlations at those locations where more severe lodging occurred. Without significant correlations with field lodging, a high stability among cultivars and years, correlated plant characters will not be reliable indices for selection of lodging resistant material.

The practical value of any of these indices is dependent, in addition to its correlation with lodging in the field, on the number of lines that can be easily and inexpensively evaluated. Pinthus (1973) stated that no selection index or individual plant character can replace, in the final stages of a breeding program, the assessment of lodging resistance in the field under a wide range of environmental conditions.

1.8 Conclusion

As Canadian wheat yield potential continues to increase, lodging may occur if straw strength does not accompany yield improvements. Although a reduction in height, from the introduction of dwarfing genes, has been the most successful means of increasing stem-lodging resistance on global level, a simple means of reducing height through the introduction of dwarfing genes into Canadian germplasm has, to date, not been successful. Moreover, the trend toward shorter cultivars may eventually be reversed because of the strong association between potential grain yield, plant height, and total aboveground biomass (Austin et al. 1980). Options such as cultivar blending or the use of PGRs may not be feasible in Canadian agriculture, due to quality and economic limitations. Breeding for lodging resistant high yielding wheat cultivars remains an important objective in western Canadian agriculture.

1.9 Statement of purpose

Cereal breeders have long sought a reliable selection technique for identifying lodging resistant genotypes. Currently, western Canadian wheat breeders rely on visual lodging scores to discard lodging susceptible lines. An artificial lodging technique has proven successful in barley (Briggs 1990), but its suitability in wheat has not been assessed. In screening trails, natural lodging may not indicate the true potential of a genotype and therefore it is important to evaluate currently grown cultivars in Canada for their potential to lodge with a specific screening technique. The presence of strong, reliable associations between culm traits and lodging would aid in selecting for lodging resistance. Global sources of straw strength may be available. Identification of suitable sources is needed to increase genetic lodging resistance into Canadian wheat to maintain yield stability achieved from past breeding efforts.

The objectives of the present thesis research are:

1) To determine a suitable, efficient method to screen for lodging susceptibility in spring wheat
2) To evaluate lodging susceptibility in Canadian and other spring wheat germplasm
3) To evaluate the effect of lodging on grain yield and quality
4) To determine whether lodging tolerant and susceptible genotypes differ in culm anatomy
5) To determine whether an environmental scanning electron microscope (ESEM) is an efficient method to screen for internal culm characters associated with lodging susceptibility
6) To evaluate bread wheat genotypes for incorporation into the western Canadian hard red spring wheat breeding program to improve genetic lodging resistance

The underlying null hypotheses tested were:

1) Lodging scores of the artificially induced lodging and/or doubled seeding rate do not differ from the control (single seeding rate)
2) Germplasm of different origins, quality classes and plant architectures do not differ in lodging susceptibility
3) Lodging does not affect grain yield and quality
4) Lodging tolerant and susceptible genotypes exhibit similar morphological/anatomical culm characters
5) The method of internal culm measurement (i.e. ESEM vs. caliper) does not differ
6) No genotypes are suitable to incorporate into western Canadian hard red spring wheat germplasm, as they do not exhibit the appropriate disease resistance, earliness, grain yield & quality acceptable for bread wheat cultivars

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2.0 Assessing lodging susceptibility in spring wheat breeding programs[2]

2.1 Introduction

Lodging in cereals refers to the displacement of culms from an upright position. Grain yield reduction in cereals almost always follows lodging, with the magnitude of loss dependent on the cultivar, growth stage and severity of lodging (Fischer and Stapper 1987; Jedel and Helm 1991). Reductions in kernel number, kernel weight and/or test weight have been reported as a direct result of lodging in winter wheat (Laude and Pauli 1956; Weibel and Pendleton 1964) and barley (Day 1957; Briggs 1990). Easson et al. (1993) reported that in UK semi-dwarf winter wheat, for each 10% increase in lodging severity, there were five fewer kernels spike^{-1} and kernel weight was reduced 2 mg, with an overall grain yield reduction of 1 t ha^{-1}.

Lodging is caused by weak culms and/or weakly anchored roots, either genetically inherent or the result of insect or disease infestations (Pinthus 1973). External forces such as wind, rain or hail reveal structural weaknesses, initiating a lodging event. Agronomic factors such as increased fertilization and/or high seeding rates tend to enhance lodging in wheat genotypes with inherent susceptibility to lodging through increased plant density (Stapper and Fischer 1990; Easson et al. 1993; Kaur et al. 2001). There has been a global improvement in lodging resistance in wheat over the last 40 years due to a reduction in plant height, primarily through the incorporation of dwarfing genes (Worland and Snape 2001).

With a significant reliance on the export market, Canada has focused on developing a consistent, uniform supply of grain, while continually adapting to customer quality needs. Breeders have focused on such traits as early maturity and disease resistance to ensure yield stability and marketing agencies have developed various grain quality classes to meet consumer preferences. Most Canadian bread wheat cultivars descend from Marquis, which was released in 1909 (DePauw and Hunt 2001). The quality attributes of this tall cultivar set the benchmark standards for bread wheat cultivars in Canada (Morrison 1960). Over the subsequent 90-yr period of wheat breeding, Canadian Western Red Spring (CWRS) cultivars have maintained Marquis' exceptional quality while increasing yield potential 6-9 kg ha^{-1} yr^{-1} (McCaig and

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DePauw 1994). However, average Canadian wheat yield (2.2 t ha^{-1}) is below the global average of 2.7 t ha^{-1} (FAO 2003). Despite attempts to develop Canadian semidwarf bread-quality cultivars, the substantial increase in yield potential from the incorporation of dwarfing genes results in grain protein levels too low for CWRS quality standards (R. DePauw, personal communication). As a result, little or no change in plant height of Canadian bread wheat cultivars has occurred over the last century of wheat breeding (McCaig and DePauw 1994). With considerable genetic variation existing worldwide for further yield improvements, incorporating genetic lodging resistance is becoming an important objective to ensure yield stability in high yielding environments due to the close association between high yields and the occurrence of lodging.

Canadian wheat breeders generally collect lodging data on breeding lines using a rating scale either following randomly-occurring lodging events, or at the end of a given growing season. Data describing lodging resistance of Canadian cultivars and advanced breeding lines are collected from Cooperative field trials conducted over multiple sites throughout western Canada. Given the often random appearance of weather events that induce lodging, however, natural lodging assessments in the field rarely provide repeatable information regarding the lodging potential of a given genotype. There are no commonly used procedures to screen for lodging susceptibility in advanced material within Canadian breeding programs.

Various techniques have been described to artificially induce lodging. Bauer (1964) made use of wind tunnels to evaluate the level of lodging resistance in wheat. Harrington and Waywell (1950) induced lodging by exposing plots individually to strong wind produced by an airplane propeller. Laude and Pauli (1956) induced lodging by manually bending and pinching the stems between their fingers, inflicting lodging from stem elongation until field maturity. Sisler and Olson (1951) introduced a technique to artificially induce permanent lodging, which was later used by other researchers in various cereal crops (Pendleton 1954; Day 1957; Day and Dickson 1958; Weibel and Pendleton 1964; Fischer and Stapper 1987; Setter et al. 1997). A wire mesh was installed over the plot and the crop was allowed to grow up through the mesh. At predetermined growth stages, varying degrees of lodging were imposed by horizontally moving the wire mesh so that plants were leaning at predetermined angles. Complete lodging was induced by gently forcing the plants over with a board, and thereafter affixing a wire mesh overtop of the plants, securing it to ensure plants remained flattened until harvest. Stanca et al. (1979) followed a similar method to completely flatten barley plots, either temporarily or

permanently, thereby inflicting varying degrees of lodging severity. The permanent lodging method, however, does not allow for the collection of data on lodging differentials among genotypes, nor does it allow for determination of lodging recovery. The effect of permanent lodging may overestimate potential yield loss. Furthermore, the time required to administer such techniques to a large number of lines in a breeding program is substantial.

A simple artificial lodging test was proposed by Briggs (1990) to obtain improved lodging data in barley breeding programs. Lodging was induced by completely flattening the middle rows of the plot by dragging a weighted plywood board, mounted on 6-cm skids, across the length of each plot. Jedel and Helm (1991) used a similar apparatus, which also progressively pushed down the crop in one direction with minimal stem breakage occurring. Both Briggs (1990) and Jedel and Helm (1991) suggested this technique would be useful for the selection of lodging resistant genotypes in a breeding program, as it requires few resources in terms of equipment, time and skill. In addition, this screening technique allows for the assessment of recovery, and potential yield losses directly from lodging for a given genotype.

The use of this technique may aid wheat breeders in differentiating between lodging susceptible and resistant genotypes and to identify sources of lodging tolerance. Little information has been published on the effect of lodging on modern Canadian spring wheat cultivars. The objectives of the present study were: 1) to determine a suitable, efficient method for the selection of lodging resistance in wheat, either by artificially induced lodging or through the use of high seeding rates, 2) to evaluate the level of lodging resistance in a wide array of wheat germplasm, and 3) to evaluate the effect of lodging on grain yield and quality in modern spring wheat genotypes.

2.2 Materials and methods

We conducted field trials in 2000, 2001 and 2002 at the Edmonton Research Station, Edmonton, Alberta (53° 34' N, 113° 31' W) (Table 1). Fertility levels of the Orthic Black Chernozemic soil (Clayton et al. 1977) were adequate to optimal in the first two study years. In 2002, fertilizer (73 kg ha^{-1} N as 46-0-0 and 34 kg ha^{-1} P as 8-24-24) was broadcast and harrowed immediately prior to planting to achieve recommended crop fertility levels. Soil nutrient status prior to planting is provided in Appendix 6.1. Moisture availability was sufficient during 2000, however, the following two years experienced moisture deficits. Irrigation was required in the spring of 2001 for germination, and record drought conditions were recorded in 2002 (Table 2.1).

The experiment was seeded into chemical fallowed land that was cultivated and then harrowed prior to seeding. Each plot was four rows wide (23 cm row spacing) and 6 m long, seeded with a self-propelled plot drill. Following emergence, weeds were controlled with MCPA Amine 500, applied at the recommended crop rate and stage (AAFRD 2002a).

The experiment was planted as a split plot arrangement of a randomized complete block design, with four blocks. Wheat genotypes were the main plots and lodging treatments the subplots. Twenty-five wheat genotypes (both cultivars and breeding lines) were included, representing a variety of origins, quality classes and plant architecture (Table 2.2). Many included genotypes were from a global search for increased straw strength. The Canadian Prairie Spring (CPS) cultivar Oslo was the strongest strawed wheat ever noted within the University of Alberta wheat breeding program over the last 30 years (K. G. Briggs, unpublished data).

The four experimental treatments included 1) a control treatment of the recommended local seeding rate (250 seeds m^{-2}) and no artificial lodging treatment applied (*control*); 2) a doubled seeding rate (500 seeds m^{-2}) and no artificial lodging treatment applied (*seedx2*); 3) a seeding rate of 250 seeds m^{-2} with an artificial lodging treatment applied at the mean early milk growth stage of the entire experiment (growth stage 73, Zadoks et al. 1974) (*GS73-E*), 14 days following the mean heading date of all 25 genotypes (see Table 1 for application dates), and; 4) a seeding rate of 250 seeds m^{-2} with an artificial lodging treatment applied at the early milk stage of each genotype (*GS73-G*). Artificial lodging was induced by pulling a weighted plywood apparatus (Briggs 1990) lengthwise across the entire 4 rows of the plot, resulting initially in the complete flattening of plants (Appendix 6.2). Lodging was scored on a scale of 1 to 9, with 1 representing no lodging (crop standing at 90°) and 9 representing a completely flattened plot (Appendix 6.3). Plots were scored immediately following a given artificial lodging application. Thereafter, all plots were scored at weekly intervals until harvest. Tolerance and susceptibility are terms used to describe the physical reaction to artificially induced lodging. Genotypes that scored between 1-3 were considered as lodging tolerant; genotypes that scored between 7-9 were considered as lodging susceptible.

Following stem elongation, plant height was recorded from the soil surface to the tip of the spike, excluding awns, for the control treatment only. Prior to harvest, ten spikes per plot were randomly collected from each plot to determine kernel number $spike^{-1}$ and kernel weight. In 2000, plots were trimmed back to 5-m and the middle two rows were hand harvested with a sickle as each plot matured. Harvested material was bagged, dried at 60°C and threshed using a

stationary thresher. In subsequent years, a plot combine harvested the entire 4 row x 6 m plot for yield, which was determined after the sample was cleaned and dried. In all three years, nearly all grain was recovered, even in severely lodged plots. Test weight was determined from a 550-ml sub-sample. Vandalism in early September 2000 resulted in the loss of one block for yield and related data in that year. Kernel number spike^{-1} was not recorded in 2000.

Data were analyzed by analyses of variance (ANOVA) performed within the PROC GLM procedure of SAS (SAS Institute, Inc. 1989). In two of the three years of study precipitation was below average, with less than half of the normal rainfall received in 2002 (Table 2.1). With such low moisture levels and plant height averaging 40% shorter than in 2000 (Appendix 6.13; 6.15), no lodging (natural and/or artificial) occurred in 2002 (Table 2.3). Year 2002 was thus dropped from entire lodging analyses. Preliminary analyses revealed significant ($P < 0.01$) year × treatment interactions for lodging scores in 2000 and 2001. Lodging treatment data were not combined over the two years due to heterogeneous error variances, as determined through the F-test for homogeneity of error variances (Gomez and Gomez 1984). Year × genotype interactions were not significant for all measured traits except plant height. In combined year analysis, genotypic effects accounted for 65% of the total sum of squares for plant height, while the genotype × year interaction effect accounted for only 3% and no rank reversals occurred (Appendix 6.8). All genotype data were thus combined over the two years.

Treatment and genotypic differences are discussed only when $P < 0.01$. The standard error of the difference between two least-square means is presented throughout (Steel et al. 1997). Single degree of freedom contrasts were employed within ANOVA to compare lodging treatments. Residuals off ANOVA from lodging data were tested for normal distribution using the Shapiro-Wilk statistic (Daniel 1990) and were normally distributed. For simple effects analysis of genotype within each treatment-year combination, lodging data were nevertheless analysed by Friedman's two-way ANOVA by ranks, with genotypes considered as treatments to determine genotypic differences. For such analyses, multiple comparisons were conducted using an experiment-wise error rate of $\alpha = 0.15$ (Appendix 6.4). This analysis has 95% power compared to simple ANOVA and may be more appropriate for rank data (Daniel 1990). To determine rank reversals between the two artificial lodging treatments in each year and between each treatment over the 2 years, Friedman's two-way ANOVA by ranks was again employed, with blocks considered as the lodging treatment or year and the genotype least-square means as treatment effects for each year separately (Daniel 1990). To determine differences between time

of scoring for lodging (i.e. initially after treatment application vs. prior to harvest), Wilcoxon two-sample test of rank sums employing PROC NPAR1WAY of SAS (SAS Institute, Inc. 1989) was employed (Table 2.5; Appendix 6.5). The EXACT option was included to generate exact *p*-values, instead of asymptotic *p*-values of the Z or t distribution, as the data set was small and ties occurred. A one-sided hypothesis was employed, testing whether lodging scores improved over time.

Genotypic correlations (Fehr 1987) between various agronomic traits were calculated from yearly genotypic least-square means. Spearman correlation coefficients (Daniel 1990) of lodging score data and Pearson Product Moment correlation coefficients of phenotypic data were employed (Steel et al. 1997) for correlation analyses of integral-scale recorded data. Valid estimates of heritability can only be made on randomly selected genotypes within a population. Fehr (1987) suggested that the term "repeatability" be used to describe the ratio of genotypic variation to phenotypic variation in a non-randomly selected group of genotypes. Measures of broad-sense repeatability for each lodging treatment over the years 2000 and 2001 were estimated using the formula described by Fehr (1987). Regression equations describing the relationship between grain yield, test weight and lodging were modeled from data calculated as percent loss from the control. Linear, quadratic and cubic equations were calculated to determine best fit (Freund and Littell 1991).

2.3 Results

Treatments differed ($P < 0.01$) for lodging in 2000 and 2001 (Table 2.3). Lodging scores were low when no artificial lodging treatments were applied as little natural lodging occurred (even at double seeding rates in 2001). Of the 25 genotypes screened, not one scored above 3 for the control treatment (recommended seeding rate; no artificially induced lodging) in 2000 and genotypes did not differ when given this treatment (Table 2.4). Heavy rain during a mid July thunderstorm did cause some natural lodging in the seedx2 treatment (doubled seeding rate; no artificially induced lodging) for taller genotypes in 2000. In many instances these ratings were related to scores from both artificial lodging treatments, with the exception of the genotypes 9107-BT04B and 9007-FH01C2 (Table 2.4). In 2001, only 2 genotypes (McKenzie, 9107-BT04B) rated above 3 for the control treatment. McKenzie rated similar under both seeding rates and 9107-BT04B rated slightly better under seedx2, with a score of 3 in that year.

Artificially inducing lodging generated a wide range of responses among the genotypes screened (Table 2.4). Low to moderate scoring cultivars were short and either had the ability to resist lodging immediately following treatment application or had the ability to recover over time (Table 2.5; Appendix 6.5). Genotypes that scored high for artificially induced lodging were tall, unable to resist artificial lodging and had little or no ability to recover, with many exhibiting greater lodging as the growing season progressed. In most cases, artificially lodged genotypes were within their published lodging category (Table 2.2). Laser was an exception, averaging an artificial lodging score of 7, but was previously rated an excellent (EX) cultivar for lodging resistance.

Though lodging scores were generally greater in 2001, the response of most genotypes to the two artificial lodging treatments was similar in 2000 and 2001. Year × treatment interaction was significant for both artificially induced lodging treatments, but accounted for only 0.3% of the total sums or squares (data not shown). Crossover interactions did occur between years for 2 genotypes, Sapphire (GS73-E) and ND965 in both lodging treatments (Table 2.4).

Mean lodging score at maturity for the 25 genotypes did not differ between artificial lodging applied at either GS73-E (mean early milk stage of the entire experiment) or GS73-G (early milk stage for each genotype) in 2001 (Table 2.3). Statistical differences between the artificial lodging treatments in 2000 were attributable to rank reversals that occurred in Sapphire, AC 2000 and AC Domain. The remaining 22 genotypes maintained similar rank positions between the two artificial lodging treatments in that year. When lodging scores are rounded to whole numbers, both artificial lodging treatments in 2000 had a mean of 5 (Table 2.3). Genotype mean lodging scores between the two artificial lodging treatments were strongly correlated in both years ($r_{2000} = 0.87$; $r_{2001} = 0.84$; $P < 0.01$).

Artificial lodging scores were moderately to strongly associated with natural lodging scores (Table 2.6). However, when severe natural lodging occurred, no association was found when plots were artificially lodged at GS73-G. Lodging scores obtained from artificially lodged treatment at GS73-E had stronger associations with natural lodging in both seeding rates in 2000 and 2001. Broad-sense repeatability was calculated for each treatment to determine whether selection potential (as measured by repeatability estimates) was different under the 4 treatments. Estimates were 16% (control), 35% (seedx2), 65% (artificial lodging at GS73-E) and 59% (artificial lodging at GS73-G), indicating that selection potential was greatest under artificial lodging at GS73-E.

Genotypes differed ($P < 0.01$) for kernel number spike^{-1}, kernel weight, test weight and grain yield when artificially lodged at GS73-E (Table 2.7). On average, artificially induced lodging at GS73-E decreased kernel number spike^{-1}, kernel weight, test weight, and grain yield by 5%, 11%, 4% and 26% relative to the control treatment, respectively. That resulted in a reduction of 2 kernels spike^{-1}, 4 mg kernel^{-1}, 3 kg hL^{-1} test weight, and 1.28 t ha^{-1} for grain yield. The ability of a particular genotype to resist or recover from artificially induced lodging at GS73-E resulted in minimal losses, particularly for kernel weight and test weight. Those genotypes unable to resist and/or recover from artificially induced lodging experienced significant reductions in kernel weight, test weight and grain yield.

Grain yield reductions from artificially induced lodging were greater than 10% for all genotypes except 4837.04 and Kohika (the two lowest scoring genotypes). Yield reductions as high as 42% occurred with high scoring genotypes, and most such yield reductions could be attributed to decreased kernel weight (Table 2.7). A high reduction of 21% in kernel weight was recorded for the breeding line 9207-DB3*E2 and high scoring cultivars had kernel weight reductions of up to 17%. On average, 2 kernels spike^{-1} were lost from the artificial induction of lodging at GS73-E, but significant genotypic differences were also found. Grain quality was moderately affected by lodging, with reductions as high as 8% recorded for test weight.

Associations were evident between lodging scores at maturity, plant height, kernel number spike^{-1}, kernel weight, test weight and grain yield under artificially induced lodging (Table 2.8). Lodging score was negatively associated with kernel number spike^{-1}, kernel weight, test weight and grain yield. Taller plants were associated with high lodging scores, a low number of kernels spike^{-1}, and low test weight and grain yield. Higher grain yield was associated with increased kernel number spike^{-1}, kernel weight, and test weight. Linear regression analyses were employed to describe the associations between lodging scores (x) and grain yield and test weight reductions from the control, and can be described by 2 equations:

1) Yield reduction (%) = $3.96 + 4.10x$ (R^2=0.80; $SE_{intercept}$=0.43)

2) Test weight reduction (%) = $0.32 + 0.71x$ (R^2=0.62; $SE_{intercept}$=0.12).

In other words, a moderately lodged crop (score = 4) may lose 20% yield and 3% test weight, whereas a completely flattened crop (score = 9) may lose up to 40% yield and 7% test weight, based on our study results.

2.4 Discussion & conclusions

Canadian wheat breeders currently rely on information gathered following naturally induced lodging events to evaluate the level of lodging resistance of any given genotype. With the random nature of natural lodging (also observed in this study), such ratings may not represent true lodging potential of a given genotype. The low level of natural lodging that occurred during the 3 years of study made it impossible to differentiate between genotypes at this treatment level.

To increase selection pressure, we explored different means to artificially induce lodging. It is well established that lodging is enhanced through increased plant density (Stapper and Fischer 1990; Easson et al. 1993) and a high seeding rate was therefore evaluated for its potential to induce lodging under recommended crop fertility. Doubling the seeding rate does not require any increased preparation time or specialized equipment within a breeding program. Results from our study indicate that simply doubling the seeding rate is an unreliable screen for lodging susceptibility. The occurrence of lodging under this treatment was dependent upon the presence of appropriate weather conditions to induce lodging, which were sporadic, unpredictable and therefore unreliable. In previous studies, researchers have applied abundant nitrogen to increase the probability of a lodging event (Malkani and Vaidya 1956). This practice, however, is also dependent upon the presence of weather conditions to induce a lodging event.

Artificially inducing lodging by pulling a weighted plywood apparatus lengthwise across the plot was effective to consistently produce a range of lodging scores among genotypes, enabling one to differentiate between them in the first two years of the study. A three-fold increase in repeatability estimates indicates artificial lodging treatments were more capable of discerning genetic differences among genotypes than a recommended seeding rate treatment. However, under severe drought conditions (2002), this artificial lodging technique was unable to differentiate between genotypes (as no lodging occurred) and therefore was not a reliable screen for lodging susceptibility in that year. Even under a severe lodging treatment, the occurrence and/or severity of a lodging is dependent upon climatic conditions of the growing season.

Trends between the two artificial lodging application methods were similar and both were related to natural lodging, with the exception of artificially induced lodging at GS73-G and severe natural lodging that occurred in the doubled seeding rate in 2000. Applying artificial lodging at GS73-G required 10 days for treatment application, whereas artificial lodging at GS73-E was applied in one day. Artificially inducing lodging at GS73-E is therefore a more practical

procedure to screen large numbers of genotypes within a breeding program for lodging susceptibility.

Hess and Shands (1966) used a similar technique to evaluate lodging susceptibility of oat genotypes from a number of populations. This 'snap test' involved pressing a handful of plant towards the plot alley and allowing them to return to the upright position. The force required to displace a handful of culms to a reclining position, and rapidity and resilience of the culms to return were recorded on a 0 (very weak) to 10 (very strong) scale. They reported snap scores were more heritable than field lodging percentages, with heritability estimates from snap scores greater than 50%. Field lodging percentages and snap scores were closely related and on the basis of intergenerational comparisons and genotype × environment interactions, they reported snap scores were more repeatable and lines were more accurately characterized by the technique (Hess and Shands 1966).

Artificially inducing lodging also demonstrated the effect of lodging on yield, though reduction assessments may have been underestimated in this study. Nearly all grain was retrieved from the ground of severely lodged plots with our equipment, but this may not be possible with larger implements used in commercial operations. Reductions in grain yield were attributed to losses in kernel number spike^{-1} and kernel weight. Physical grain quality was adversely affected through reductions in test weight. Such reductions in kernel number spike^{-1}, kernel weight, grain yield and test weight have been previously reported for wheat, all of which were dependent on the growth stage, lodging severity and cultivar (Pumphrey and Rubenthaler 1983; Fischer and Stapper 1987; Easson et al. 1993).

Lodging at the early milk stage was reported by Jedel and Helm (1991) to be the growth stage that maximized potential yield losses from lodging and enabled the selection of more tolerant barley lines. Briggs (1990) also reported severe yield losses at this stage, but some barley cultivars were able to recover from artificially induce lodging over time. Pinthus (1973) indicated the cereal growth stage at which lodging is scored may also be important, particularly if the crop is able to recover from lodging. If plots are only scored once before harvest, one may underestimate the lodging potential of genotypes that had lodged earlier in the season, but then recovered before scoring.

In the present study, most wheat genotypes did not display the ability to recover following lodging that was recorded in barley genotypes by Briggs (1990). However, 4837.04, Kohika, 9207-DB3*E2 and 9207-DB3*D and AC 2000 did recover, most likely through

geotropic cellular enlargement as described by Bridges and Wilkins (1973). This ability to regain an erect position allows for the return of favorable light interception. The extent of yield loss is dependent upon how rapidly and to what extent the genotype is able to recover. Although these genotypes were able to moderately recover from severe lodging and ease commercial harvesting, the effects on grain yield and quality were not avoided, particularly in 9207-DB3*E2. With a final average lodging score of 5 for 9207-DB3*E2, this genotype experienced reductions above the experimental average for kernel number spike^{-1} and test weight, exhibited the highest reduction for kernel weight and had a yield reduction similar to severely lodged genotypes.

Artificially inducing lodging allowed an evaluation of each genotype's lodging potential. Most lodging tolerant genotypes in the present study were semidwarfs of non-Canadian origin. The positive correlation between plant height and lodging reported here has also been reported by other researchers examining a diverse range of cereal genotypes (Murthy and Rao 1980; Keller et al. 1999), with many researchers also reporting semidwarf cultivars as the most lodging tolerant lines (Stanca et al. 1979; Briggs 1990; Stapper and Fischer 1990; Jedel 1991). All Canadian bread wheat genotypes examined in this study were of conventional height, were unable to resist lodging, and showed little or no ability to recover.

Lodging can cause significant economic losses in grain yield and quality of western Canadian bread wheat, and may interfere with the speed and efficiency of harvest. Agronomic options exist to prevent lodging, but such options as cultivar blending (Jackson and Wenning 1997) or the use of plant growth regulators (Easson 1992) may not be feasible in western Canadian agricultural systems, due to grain quality standards and financial limitations in wheat production. The most cost-effective, sustainable and long-term solution to lodging is the development of resistant cultivars. From the results of this study, we identified two lodging tolerant genotypes (4837.04 and C9800L-015) and they are presently being incorporated into elite western Canadian bread wheat germplasm in an effort to increase genetic lodging resistance.

2.5 Summary

Considerable genetic variation remains for further yield improvement in Canadian hard red spring wheat (*Triticum aestivum* L.) and it is therefore becoming more important to improve genetic lodging resistance in high yielding environments as crops may be more prone to lodge. Consistent selection for lodging resistance under natural conditions is difficult due to the sporadic and often random nature of lodging events. We conducted field trials in Edmonton, AB, Canada

(2000 – 2002) to determine if either a high seeding rate, or artificially inducing lodging (by dragging a weighted apparatus across plots at the early milk stage) would be effective in classifying inherent lodging susceptibility of wheat genotypes, and to determine the effect lodging has on grain yield, yield components and test weight. For the 25 genotypes tested, applying artificial lodging at the mean early milk growth stage for the genotypes was a suitable method to screen and identify lodging tolerant and susceptible genotypes. Tolerance to artificially induced lodging was mainly found within semi-dwarf genotypes and susceptibility was found mainly within Canadian bread wheat genotypes. Severe lodging resulted in yield losses as high as 42%, coupled with an 8% reduction in test weight. Lodging tolerant genotypes identified in this study are now being crossed with elite Western Canadian bread wheat in an effort to increase genetic lodging resistance within Canadian germplasm.

2.6 Tables

Table 2.1. Seeding dates, dates of artificially induced lodging (applied at the mean early milk stage of entire experiment) and harvest dates, and accumulated precipitation (mm) over the growing season for a lodging experiment planted at Edmonton, AB (2000-2002).

	Date			Precipitation[z] (mm)					
Year	Seeding	Artificial lodging	Harvest	May	June	July	August	September	Total
2000	05-May	19-Jul	30-Aug	74	70	99	36	51	330
2001	10-May	24-Jul	10-Sep	25	55	150	25	21	276
2002	08-May	15-Jul	31-Aug	17	21	35	52	10	135
Normal[y]				49	87	92	69	44	341

[z]Data collected from University of Alberta, Edmonton Research Station.
[y]Data obtained from Environment Canada (2002); Canadian Climate Normals for Edmonton City Center (1971-2000).

Table 2.2. Origin, quality class, plant architecture and lodging rating scale from published literature for 25 genotypes grown at Edmonton, AB (2000-2002).

Genotype	Origin[z]	Quality class[y]	Plant Architecture	Lodging rating[x] from literature
4837.04	NZ	Bread	Semidwarf	-
Kohika	NZ	Bread	Semidwarf	G
C9800L-048[w]	CIMMYT/SPARC	HYV	Semidwarf	-
Oslo	NAPB	CPS-R	Semidwarf	EX
Otane	NZ	Bread	Semidwarf	G
Sapphire	NZ	Bread	Semidwarf	-
C9800L-015[w]	CIMMYT/SPARC	HYV	Semidwarf	-
AC Foremost	SPARC	CPS-R	Semidwarf	EX
N93-0119	NAPB	CWRS	Semidwarf	G
9207-DB3*E2[w]	SPARC	CWRS	Tall	-
9207-DB3*D[w]	SPARC	CWRS	Tall	-
AC 2000	SPARC	CPS-W	Semidwarf	EX
ND695	NDSU	CWRS	Semidwarf	G
AC Domain	CRC	CWRS	Tall	VG
AC Intrepid	SPARC	CWRS	Tall	G
AC Vista	SPARC	CPS-W	Semidwarf	G
Laser	UA	CWES	Tall	EX
9007-FB01C[w]	SPARC	CWRS	Tall	-
McKenzie	SWP	CWRS	Tall	F
AC Barrie	SPARC	CWRS	Tall	G
9107-BT04B[w]	SPARC	CWRS	Tall	-
AC Splendor	CRC	CWRS	Tall	F
9007-FH01C2[w]	SPARC	CWRS	Tall	-
9007-FH01C4[w]	SPARC	CWRS	Tall	-
9007-FH01D3[w]	SPARC	CWRS	Tall	-

[z]NZ = New Zealand; CIMMYT = International Maize and Wheat Improvement Centre (Mexico); SPARC = Semiarid Prairie Agricultural Research Centre (Swift Current, Canada); NAPB = Nickerson American Plant Breeders Inc. (Colorado, USA); NDSU = North Dakota State University (ND, USA); CRC = Cereal Research Centre (Winnipeg, Canada); UA = University of Alberta (Edmonton, Canada); SWP = Saskatchewan Wheat Pool (Saskatoon, Canada).

[y]Bread = type in New Zealand; HYV = high yielding varieties; CPS –R or W = Canadian prairie spring – red or white; CWRS = Canadian western red spring.

[x]AAFRD 2002b; NZCFR 2000; MAES 2002; EX = excellent, VG = very good, G = good, F = fair.

[w]Canadian breeding line.

Table 2.3. Mean lodging scores of seeding rate treatments and artificially induced lodging treatments (either applied at mean early milk stage of entire experiment or early milk stage of each genotype) for 25 spring wheat genotypes grown at Edmonton, AB (2000-2002).

Treatment	Seeding rate (seeds m^{-2})	Treatment abbreviation	Lodging score[z] at maturity 2000	2001	2002
No artificial lodging					
Recommended seeding rate	250	Control	1.2*d*	1.9*b*	1.0*a*
Doubled seeding rate	500	Seedx2	2.5*c*	1.9*b*	1.0*a*
Artificially lodged					
Experiment wide	250	GS73-E	4.5*b*	6.2*a*	1.0*a*
Genotype specific	250	GS73-G	5.3*a*	6.5*a*	1.0*a*
Treatment *F*-test			**	**	ns
Treatment × genotype *F*-test			**	**	ns
SE[y]			0.2	0.1	0

**, ns - significant at $P < 0.01$ and not significant ($P \geq 0.01$), respectively.
*a-d*Means within columns with the same letter are not significantly different at $P < 0.01$, as determined from a single degree of freedom contrasts.
[z]Lodging scored on a scale of 1 to 9, with 9 = completely lodged plot.
[y]Standard error of the difference between two least-square means.

Table 2.4. Mean lodging scores at harvest for two seeding rate treatments (not artificially lodged) and artificially induced lodging treatments applied at the mean early milk stage (GS73) of the entire experiment (E) or the early milk stage of each of the 25 spring wheat genotypes (G) grown at Edmonton, AB (2000-2001).

	2000				2001				
	Seeding rate (seeds m-2)		Artificial lodging		Seeding rate (seeds m-2)		Artificial lodging		Plant height[y]
Genotype[z]	250	500	GS73-E	GS73-G	250	500	GS73-E	GS73-G	(cm)
4837.04	1	1	1	1	1	1	2	2	82
Kohika	1	1	1	1	1	1	2	3	73
C9800L-048	1	2	1	1	1	1	3	3	76
Oslo	1	1	2	2	1	1	3	3	83
Otane	1	2	3	5	1	1	3	3	79
Sapphire	1	1	1	6	1	1	5	7	85
C9800L-015	1	1	2	2	1	1	6	5	79
AC Foremost	1	1	3	3	1	1	5	7	81
N93-0119	1	2	2	4	1	1	6	7	89
9207-DB3*E2	1	1	3	3	1	2	6	6	80
9207-DB3*D	1	2	3	3	1	1	6	7	90
AC 2000	1	1	3	6	1	2	6	7	90
ND695	1	2	2	2	2	2	8	8	89
AC Domain	1	1	4	7	3	2	8	8	96
AC Intrepid	2	5	6	8	3	3	7	6	104
AC Vista	1	5	6	5	3	4	8	8	91
Laser	1	5	7	8	3	3	8	7	101
9007-FB01C	3	5	8	8	2	2	8	7	102
McKenzie	3	5	7	9	4	4	9	9	98
AC Barrie	2	3	8	8	3	3	9	9	103
9107-BT04B	1	1	7	9	4	3	9	9	107
AC Splendor	2	6	7	9	3	3	9	7	104
9007-FH01C2	1	1	8	8	2	2	9	9	108
9007-FH01C4	1	3	9	9	2	2	8	9	105
9007-FH01D3	1	5	8	9	3	2	9	9	110
Significance level[x]	ns	**	**	**	**	**	**	**	**
Chi-squared value[w]	9.2	44.1	64.8	63.4	57.3	60.7	80.6	75.1	
SE[v]	0.6	1.2	1.1	1.1	0.5	0.5	0.7	0.8	2.1

Lodging scored on a scale of 1 to 9, with 9 = completely lodged plot.

[z]Genotypes listed from lodging tolerant to susceptible, determined from GS73-E average.

[y]Height reported from least-square means off ANOVA for combined analysis of 2000-2001.

[x]Friedman's 2-way analysis of variance by ranks: **, ns - effects significant at $P < 0.01$ and not significant ($P \geq 0.01$), respectively; genotypes significantly different when the difference between the sum of their ranks is > 64.3.

[w]Critical value = 43.0 (df = 24, $\alpha = 0.01$).

[v]Standard error or the difference between two least-square means off ANOVA.

Table 2.5. Mean lodging scores immediately following artificial lodging application (initial) and just prior to harvest (final), applied at either at the mean early milk stage of the entire experiment (GS73-E) or at the milk stage of each genotype (GS73-G) of selected genotypes that exhibited varying abilities to recover over time from artificially induced lodging.

	2000						2001					
	GS73-E			GS73-G			GS73-E			GS73-G		
Genotype[z]	Initial		Final	Initial		Final	Initial		Final	Initial		Final
4837.04	2	*	1	3	*	1	5	*	2	6	*	2
Kohika	2		1	3	*	1	3		2	3		3
Oslo	2		2	4		2	4		3	3		3
Otane	5		3	6		5	4		3	6	*	3
9207-DB3*E2	7	*	3	6		3	9	*	6	9	*	6
9207-DB3*D	5		3	5		3	9	*	6	9	*	7
AC 2000	6		3	8	*	6	8		6	9	*	7
AC Domain	5		4	7		7	9		8	9		8
Laser	6		7	9		8	8		8	6		7
McKenzie	5		7	8		9	9		9	9		9
AC Barrie	7		8	7		8	9		9	9		9
AC Splendor	5	*	7	7	*	9	8	*	9	7		7

Lodging scored on a scale of 1 to 9, with 9 = completely lodged plot.

[z]Genotypes listed from lodging tolerant to susceptible, determined from GS73-E average.

*Significant difference ($P < 0.05$) between lodging scores at different rating times, determined by Wilcoxon two-sample test of rank sums by year, lodging treatment and genotype. A blank cell indicates initial and final lodging scores did not differ ($P \geq 0.05$).

Table 2.6. Spearman genotypic correlations between lodging scores from different seeding rates, and artificially induced lodging treatments for 25 spring wheat genotypes grown at Edmonton, AB (2000-2001).

	Artificial lodging at GS73-E		Artificial lodging at GS73-G	
Correlated treatments[z]	2000	2001	2000	2001
Seedx2	0.50	0.84	ns	0.64
Control	0.55	0.88	0.55	0.68

Reported correlation coefficients significant at $P < 0.01$; ns: non-significant ($P \geq 0.01$) correlation coefficient.

[z]Control = 250 seeds m^{-2}; seedx2 = 500 seeds m^{-2}; no artificial lodging applied. Artificially induced lodging at mean early milk growth stage of entire experiment (GS73-E) or early milk stage of each genotype (GS73-G); seeded at 250 seeds m^{-2}.

Table 2.7. Mean yield component traits, test weight and grain yield of 25 spring wheat genotypes artificially lodged at the mean early milk growth stage of the entire experiment (GS73-E) and percent reduction relative to non-lodged control for each genotype at Edmonton, AB (2000-2001).

		Kernels spike^{-1}		Kernel weight		Test weight		Grain yield	
Genotype[z]	Lodging at maturity	(no.)	Reduction from control[y] (%)	(mg)	Reduction from control (%)	(kg hl^{-1})	Reduction from control (%)	(t ha^{-1})	Reduction from control (%)
4837.04	1	43	-	39	3	76	1	5.22	4
Kohika	2	45	5	38	0	76	1	5.10	6
C9800L-048	2	40	8	36	0	75	1	5.08	11
Oslo	2	41	3	35	3	75	1	4.79	10
Otane	3	45	6	37	6	74	2	4.12	20
Sapphire	3	48	18	37	7	70	3	4.59	22
C9800L-015	4	37	6	33	6	75	3	5.04	16
AC Foremost	4	44	1	38	10	74	4	4.32	20
N93-0119	4	32	19	34	6	75	3	4.56	20
9207-DB3*D	5	28	11	36	13	76	4	3.28	26
9207-DB3*E2	5	35	7	31	21	71	7	2.98	36
AC 2000	5	40	1	38	14	72	5	4.16	27
ND695	5	31	3	34	11	75	3	4.39	20
AC Domain	6	27	1	32	12	73	3	3.06	28
AC Intrepid	6	28	9	36	9	73	4	3.31	28
AC Vista	7	38	7	38	15	71	5	3.99	30
Laser	7	35	5	33	14	70	7	3.41	40
9007-FB01C	8	28	9	28	10	72	5	2.74	25
McKenzie	8	32	1	27	17	70	8	2.64	42
AC Barrie	8	29	10	31	15	69	8	2.46	39
9107-BT04B	8	27	2	34	16	68	8	2.54	35
AC Splendor	8	27	9	33	13	70	6	2.88	28
9007-FH01C2	8	32	3	33	15	74	5	2.51	37
9007-FH01C4	9	33	-	31	14	74	5	2.64	39
9007-FH01D3	9	32	4	31	14	74	4	2.34	39
Mean			*5*		*11*		*4*		*26*
Genotype *F*-test		**		**		**		**	
Genotype × year *F*-test		-		ns		ns		ns	
SE[x]		2.2		1.2		1.5		0.30	

ns, **: not significant ($P \geq 0.01$) and effects significant at $P < 0.01$, respectively.

[z]Genotypes listed from lodging tolerant to susceptible, determined from GS73-E average.

[y]No artificial lodging applied; seeded at recommended rate.

[x]Standard error or the difference between two least-square means.

Table 2.8. Pearson (Spearman) genotypic correlation between lodging score, plant height, yield component traits, test weight and grain yield for 25 spring wheat genotypes artificially lodged at the mean early milk stage of the entire experiment (GS73-E) at Edmonton, AB (2000-2001).

Correlated traits	Lodging at maturity	Plant height	[z]Kernel number spike^{-1}	Kernel weight	Test weight
Plant height	(0.58)				
[z]Kernel number spike^{-1}	(-0.73)	-0.76			
Kernel weight	(-0.70)	ns	0.66		
Test weight	(-0.55)	-0.48	ns	ns	
Grain yield	(-0.90)	-0.45	0.73	0.69	0.47

Reported correlation coefficients significant at $P < 0.01$; ns: non-significant ($P \geq 0.01$) correlation coefficient.

[z]Based on one year of data.

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3.0 The association of culm anatomy with lodging susceptibility in modern spring wheat genotypes[3]

3.1 Introduction

Lodging in cereals refers to the displacement of culms from an upright position. Lodging derives either from roots, resulting in plants flattening at ground level, or from stems, where culms usually bend or break at basal internodes (Pinthus 1973). Grain yield reductions almost always accompany lodging, with the magnitude of loss dependent on the cultivar, growth stage and severity of lodging (Fischer and Stapper 1987; Jedel 1991; Easson et al. 1993). Lodging can reduce profitability through reduced grain yield, delayed harvest, increased drying costs and/or reduced grain quality. Lodging is most detrimental when it occurs at heading, or those growth stages immediately following heading. Lodging during this time period will affect both kernel number spike^{-1} and kernel weight, whereas a later induction of lodging (i.e. soft dough to maturity) primarily affects kernel weight (Laude and Pauli 1956; Weibel and Pendleton 1964; Briggs 1990; Kelbert et al. 2003 submitted to Plant Breeding).

A global improvement in lodging resistance in wheat has occurred over the last 40 years as a result of a reduction in plant height (Fisher and Wall 1976; Cox et al. 1988), primarily due to the incorporation of dwarfing genes (Worland and Snape 2001). Modern, high-yielding cultivars, are generally shorter, with stronger straw, exhibit a higher harvest index and are thus responsive to high fertilizer input.

Most Canadian Western Red Spring (CWRS) bread wheat cultivars descend from the cutlivar Marquis, which was released in 1909 (DePauw and Hunt 2001). This tall cultivar set benchmark quality standards for bread wheat cultivars in Canada (Morrison 1960). Over the subsequent 90-yr period of wheat breeding, hard red spring wheat (CWRS) cultivars have maintained Marquis' exceptional quality while increasing yield potential 6-9 kg ha^{-1} yr $^{-1}$ (McCaig and DePauw 1994). With evidently considerable genetic variation existing for further yield improvements, it is becoming more important to incorporate genetic lodging resistance into

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cultivars grown in high yielding environments. Despite attempts in developing Canadian semidwarf bread-quality cultivars, the substantial increase in yield potential from the incorporation of dwarfing genes results in grain protein levels too low for CWRS quality standards (R. DePauw, personal communication). As a result, little or no change in plant height has occurred in CWRS wheat over the last 90 years (McCaig and DePauw 1994).

Stem lodging is caused by weak culms, genetically inherited, or as the result of insect or disease infestations (Pinthus 1973). External forces such as wind, rain or hail reveal the weakness of the stems and initiate the onset of lodging. Agronomic factors such as increased fertilization and/or high seeding rates are known to enhance severity of lodging in wheat (Stapper and Fischer 1990; Easson et al. 1993; Kaur et al. 2001). Berry et al. (2000) conducted a study in the UK to determine the effect of various agronomic practices on plant characters related to lodging in winter wheat. They reported that combinations of reduced spring nitrogen, low residual nitrogen levels, and delayed sowing reduced plant height and increased basal stem strength through increased stem diameter and culm wall thickness. These changes in plant morphology increased the minimum wind speed at which a given plant would lodge. However, Berry et al. 2000 concluded that agronomic practices compatible with high yields (i.e. higher seeding rate, earlier date of planting and elevated nitrogen levels) were not compatible with resistance levels required to withstand the potentially high wind gusts encountered in the UK. Combining straw strength with other desirable characteristics, therefore, remains an important breeding objective for high yielding environments.

Under natural field conditions, lodging occurs sporadically, making it difficult to select lodging resistant lines in early generations of selection. The identification and selection for correlated traits has been a goal of many breeders, and many have found differences among lodging resistant and susceptible genotypes for various morphological and anatomical culm characters. The importance of short stature to enhance lodging resistance is well established. However, height may not be the only factor contributing to the level of stem lodging resistance, even in post Green Revolution genotypes (Easson et al. 1993). Lodging resistant and susceptible cultivars differed for basal internode lengths in barley (Stanca et al. 1979; Dunn and Briggs 1989), with resistant cultivars exhibiting shorter basal internodes. Wider basal culm diameter has been associated with lodging resistance in wheat (Mukherjee et al. 1967; Zuber et al. 1999), barley (Dunn and Briggs 1989), and oats (Jellum 1962). Such studies also reported that lodging resistant genotypes exhibited thicker culm walls than those susceptible to lodging. In a very early

investigation into factors influencing lodging, Brady (1934) reported the most significant anatomical feature related to lodging resistance was an increased number of vascular bundles. The thickness of the sclerenchyma ring has also been related to an enhanced level of lodging resistance in barley (Dunn and Briggs 1989). There have been no reports on the relationship between culm characters and lodging in modern genotypes available to Canadian wheat breeders.

Various histological techniques have been employed for the detailed observation of culm anatomy with a simple light microscope. Considerable time is required for sample preparation (i.e wax embedding for microtome sectioning) and staining (i.e. for specific chemical components). The development of the environmental scanning electron microscope (ESEM) requires no complex sample preparation, thereby avoiding the introduction of artefacts, a potential problem with the conventional scanning electron microscope (SEM) (Danilatos 1993). In addition, the accompanying software package is able to electronically measure the scanned images and compute averages, avoiding the need to manually measure individual plant characters with a micrometer eyepiece. A full discussion of the ESEM instrument is given by Danilatos (1993). The presence of a reliable association between any easily measured culm character and lodging may enhance efficient selection of lodging resistant lines in early generations.

The objectives of the present study were to determine: 1) whether culm characters differ between modern wheat genotypes of varying lodging susceptibility, 2) the association between culm characters and lodging within modern wheat genotypes available to a Canadian wheat breeder, and 3) whether an ESEM is an efficient method to screen for culm characters associated with lodging resistance.

3.2 Materials and methods

We conducted a field experiment in 2000 and 2001 at the Edmonton Research Station, Edmonton, Alberta (53° 34' N, 113° 31' W), which has been described elsewhere (see Chapter 2). Briefly, the experiment was planted as a split plot arrangement of a randomized complete block with four blocks. Wheat genotypes were planted to the main plots and lodging treatments to the subplots. Twenty-five wheat genotypes (both cultivars and breeding lines) were included in the original field experiment, representing a variety of origins, quality classes, plant architecture and perceived lodging tolerance. The two experimental treatments included: 1) a control treatment at the recommended local seeding rate (250 seeds m^{-2}) and no artificial lodging treatment applied; 2)

a seeding rate of 250 seeds m^{-2} with an artificial lodging treatment applied at Zadoks growth stage 73 (Zadoks et al. 1974), 14 days following mean heading date of the entire experiment. Artificial lodging was induced by dragging a weighted plywood apparatus on wheels lengthwise across the plots, resulting initially in the complete flattening of plants (Appendix 6.2).

Individual plots were four rows wide (23 cm row spacing) and 6 m long, seeded into chemical-fallowed land that was cultivated and harrowed prior to seeding. Moisture availability was sufficient during 2000, however irrigation was required in the spring of 2001 for germination. Following emergence, weeds were controlled with MCPA Amine 500, applied at the recommended crop stage and rate (AAFRD 2002a). Fertilizer was not applied, as soil fertility was adequate, based on soil tests.

Of the 25 genotypes included in the original field experiment, 13 were chosen for the present study, based on preliminary experimental lodging tests (Table 3.1). These 13 genotypes were sorted into 3 groups representing differential lodging susceptibility based on mean scores over the two study years: 1) four lodging tolerant (T) genotypes (mean lodging score between 1 and 3), 2) four moderately lodging tolerant (M) genotypes (mean lodging score between 4 and 6), and 3) five lodging susceptible (S) genotypes (mean lodging score between 7 and 9) (Table 2). Tolerance and susceptibility are terms used to describe the physical reaction to artificially induced lodging. In 2000 and 2001, two weeks prior to harvest, at Zadoks growth stage 87 (hard dough) (Zadoks et al. 1974), five plants were randomly sampled from within each plot of the first three blocks of the control treatment. Sampling was not done within the lodged treatment, as plants were generally not in sufficient physical condition for individual plant harvest. The following measurements were taken from the main culm of each of the 5 plants sampled per plot: *(i)* plant height (cm), measured from the crown to the tip of the spike, excluding awns; *(ii)* number of internodes (internodes < 0.5 cm in length were not counted, numbered from the ground upward); *(iii)* length of each internode (cm); *(iv)* diameter of each internode (mm), measured with a caliper. In 2001, each culm was scored for the presence of adventitious roots, developed in the intercalary meristems in the basal culm nodes. A rating scale of 0-5 was used, based on the number and size of roots, with 0 indicating no adventitious roots and 5 indicating the most developed root system. Following all whole-plant measurements, the 2nd basal internode was excised from plants of blocks one and three only, and placed in a 1:1 solution of ethanol: water and stored at 4°C. The second internode was chosen for detailed measurements as the first basal

internode has previously been found to either be too variable (Hamilton 1941) or of insufficient length to influence lodging potential (Dunn and Briggs 1989).

Following internode excision, free hand sections were made as thin as possible from the middle of each internode on four of five sample plants per plot. Each culm sample was examined with an environmental scanning electron microscope (ESEM; FEI-Phillips-Electroscan) at 25× magnification. Hydrated samples were observed at a working distance of 14.5 mm at 0.9 Torr of vacuum pressure. An accelerating voltage (the amount of energy carried by the primary electrons) of 25 kV was used for the beam to improve image quality. Proprietary gaseous electron (GSE) detector was selected. The image was saved as a .tif image under high resolution (higher than 2K), which allowed for high magnification of the section for detailed measurements. Soft Imaging Systems AnalySIS® Pro GmbH version 3.2.678 software was used to make all measurements on the culm cross sections.

The following measurements were taken on each ESEM sample: *(i)* culm diameter (mm), an average of two measurements taken at right angles to each other; *(ii)* culm wall thickness (mm), an average of four radial measurements from the epidermis to the innermost edge of parenchyma cells; *(iii)* lumen diameter (mm), an average of two measurements taken at right angles to each other, opposite to where the measurements were taken for diameters; *(iv)* sclerenchyma ring thickness (μm), an average of ten radial measurements taken, avoiding positions where vascular bundles were embedded in the sclerenchyma tissue, included the epidermis; and *(v)* number of vascular bundles, counted according to their location (sclerenchyma ring or parenchyma). To ensure the thickened cells around the periphery of the culm was the sclerenchyma ring, the sample was tested for the presence of lignin using the method described by Johansen (1940). Sections were placed on a slide in a large drop of a solution of 0.1% phloroglucin in 10 ml of 95% ethanol and covered with a cloverslip. When the majority of the solution evaporated around the coverslip, droplets of 25% HCl were placed on the slide and allowed to diffuse under the coverslip. The appearance of a red-violet color indicated the presence of lignin.

Lodging data were recorded within the experimental field trial, and were scored immediately prior to crop harvest. Lodging was scored on a scale of 1 to 9, with 1 representing no lodging and 9 a completely flattened plot. Natural lodging scores were taken from the control plot, the same plots that plants were sampled from.

Data were analyzed within combined-year analyses of variance for a randomized complete block, with sampling (Steel et al. 1997) within the PROC GLM procedure of SAS (SAS Institute, Inc. 1989). The year × block × genotype effect was employed as the error term (not the sampling error of [year × block × genotype]×sample no) and used to test the hypothesis of genotypic differences. Single degree of freedom contrasts were employed within analyses of variances (Steel et al. 1997) to separate the effect of the three predetermined groups based on lodging susceptibility. Genotypic differences are discussed only when significant differences occurred at $P < 0.05$. Least-square means and standard error of the difference between two least-square means are presented throughout (Steel et al. 1997). Phenotypic correlations were calculated on a plot basis and genotypic correlations (Fehr 1987) were calculated from yearly genotype least-square means, with the effects due to blocks removed. Spearman rank correlations were computed between each culm trait, and natural and artificially induced lodging scores.

3.3 Results

There were significant genotype × year interactions for plant height and artificially induced lodging (Table 3.2). On average, plants were 11% shorter in 2001 (86 cm) than 2000 (97 cm). In combined year analyses, genotype effects accounted for 64% of total sum of squares for height, while the genotype × year interaction effects accounted for only 3% and genotypes did not exhibit crossover interactions (Appendix 6.9). Eleven of thirteen genotypes exhibited similar artificially induced lodging scores over the 2 study years. Crossover interactions occurred for 2 genotypes, with mean artificially induced lodging scores for Sapphire and ND695 of 1 and 2 in 2000 and 5 and 8 in 2001, respectively. In combined-year analyses, however, genotype effects accounted for 62% of total sum of squares for lodging, while the genotype × year interaction effects accounted for only 6% (Appendix 6.9). Genotype main effects are therefore discussed using results combined over years for artificially induced lodging and plant height (Table 3.2).

Genotypes differed ($P < 0.05$) for both natural and artificially induced lodging, plant height, number of internodes, but not for the frequency of adventitious roots (Table 3.2). Four genotypes exhibited high levels of tolerance to artificially induced lodging (rating 2 or 3) and all four were, on average, less than 81 cm tall. Five genotypes exhibited low levels of tolerance to artificially induced lodging (rating 7 or 8) and four of the five were taller than 100 cm. Average internode number varied from 4.7 to 5.6 for the 13 genotypes. The three groupings of genotypes based on lodging susceptibility did not differ for natural lodging or internode number. The

moderately tolerant lodging (M) group had fewer mean adventitious roots than the lodging susceptible (S) group (Table 3.2).

Mean internode length across all four basal internodes was 2 cm shorter and mean internode diameter was 0.4 mm wider in 2001 than 2000 (Appendix 6.16; Appendix 6.17). Genotype × year interactions were not significant for all measured internode lengths and diameters, except for length of the first, and diameter of the third internode for which crossover interactions occurred among genotypes over years. The length of the first internode in Kohika, AC Domain, and Laser did not change over years, whereas C9800L-048, AC Foremost and AC Splendor exhibited a much shorter first internode (i.e. > 2 cm average) in 2001. The diameter of the third internode in C9800L-048, Oslo and AC Vista were thinner in 2001 then 2000, whereas all other genotypes had wider internode diameters in that year.

Genotypes differed ($P < 0.05$) for internode length (Table 3.3). On average, the lodging tolerant (T) grouping of 4 cultivars had shorter internodes than the moderately tolerant (M) or susceptible (S) lodging groupings. There was, however, no consistent relationship between each of the internode lengths for each genotype within the three groupings of lodging susceptibility. Both Kohika and Olso (two genotypes of the four chosen to represent lodging tolerant lines) consistently exhibited among the shortest internode lengths for the 3 basal internodes measured. There was no pattern among genotypes for internode length between the other two genotypes in this grouping. McKenzie and AC Barrie (two genotypes of the five chosen to represent lodging susceptible lines) consistently exhibited longer internodes at all 4 internodes. Again, there was no consistent pattern for internode length among the other 3 genotypes in this grouping.

At each of the four basal internodes, genotypes differed ($P < 0.05$) for internode diameter (Table 3.3). Although differences were not consistent over lodging groupings, both Sapphire and Kohika (rated as lodging tolerant) had wide culms at the basal internodes measured. AC Domain (rated as moderately lodging tolerant) consistently exhibited thinner culms at the first three internodes, whereas the culms of Laser (rated as susceptible) were as wide as those of Sapphire and Kohika at the third and fourth internodes. McKenzie had a wide culm diameter at the first internode and a thin culm diameter at the fourth internode.

Genotype × year interactions were not significant for all measured microscopic traits except for the number of vascular bundles in the sclerencyhma ring (Table 3.4). Genotypes differed ($P < 0.05$) for the number of vascular bundles in the sclerenchyma ring in both years, but rank reversals occurred over years for this trait. The three groupings of lodging susceptibility did

not differ for this trait in both years. Two genotypes of differing lodging susceptibility, Kohika (tolerant) and AC Splendor (susceptible), had the most vascular bundles in the sclerenchyma ring in 2001(Table 3.4).

Genotypes differed ($P < 0.05$) for the number of vascular bundles found in the parenchyma tissue, the combined total number of vascular bundles, and culm wall thickness, but not for lumen diameter or sclerenchyma ring thickness (Table 3.4). A range of 25 to 30 vascular bundles in the parenchyma tissue was observed among genotypes, contributing more than two thirds of the total vascular bundles in the culm section. The number of vascular bundles in the sclerenchyma ring was unrelated to the number found in the parenchyma tissue. Lodging tolerant genotypes Oslo and Sapphire had thick culm walls, while moderately tolerant genotypes (AC Domain) and susceptible genotypes (McKenzie) had thin culm walls (Figure 3.1). The culm wall of Laser (a susceptible genotype) was similar to the lodging tolerant Sapphire. Lodging susceptible groupings did not differ for the number of vascular bundles, thickness of the culm wall or the lumen diameter. The lodging tolerant (T) grouping had a thicker sclerenchyma ring than the moderately tolerant (M) grouping.

Culm diameter was measured by the ESEM as well as with a caliper (Appendix 6.6). Using a caliper, genotypic mean culm diameter over years was 3.14 mm. Using the ESEM, genotypic mean culm diameter over years was 3.15 mm. No statistical difference was found between the two methods. The standard error of the difference between two least-square means recorded from calliper measurements (0.17) was larger than the standard error recorded from ESEM measurements (0.15).

Plant height and the length of the 4th internode was correlated on a genotypic basis with artificially induced lodging (Table 3.5). Scores for artificially induced lodging were also phenotypically correlated with the number of internodes, but at a low level of association. Plant height and basal internode length was associated with both natural and artificially induced lodging scores on a phenotypic basis. Adventitious root frequency, internode diameter, culm wall thickness, lumen diameter, the number of vascular bundles and the thickness of the sclerenchyma ring were not correlated ($P \geq 0.05$) with natural or artificially induced lodging (data not shown).

3.4 Discussion and conclusions

Many researchers have reported associations between plant height, number of internodes, adventitious roots, basal internode length and diameter, number of vascular bundles, culm wall thickness, lumen diameter and sclerenchyma thickness with lodging (Jellum 1962; Tandon et al.1973; Stanca et al. 1979; Mukherjee et al. 1980; Murthy and Rao 1980; Dunn and Briggs 1989; Fisher and Stapper 1990; Crook and Ennos 1994; Keller et al. 1999; Zuber et al. 1999). Short plants with more short, wide internodes with thick culm walls and a high number of vascular bundles were generally characteristic of the lodging tolerant genotypes studied. Many such studies juxtaposed a small number of lodging resistant and susceptible genotypes. In the present study, three lodging resistant genotypes exhibited such morphological characteristics. Kohika had short, wide basal internodes with a high number of vascular bundles in the sclerenchyma ring. Oslo also had short basal internodes with a thick culm wall and a thick sclerenchyma ring. The culm of Sapphire was wide, with a thick culm wall. On a generalized basis, however, plant height and the length of the basal internodes were the two main culm characters closely associated with natural and artificially induced lodging for all genotypes studied. Other culm characters did not appear to be related to lodging over the 13 genotypes studied.

The precision of a correlation is based upon the quality of phenotypic lodging data, the sample size and the degree of stability of a character across environments. In addition, the use of a correlated trait for selection in a breeding program necessitates that the association be strong and predictable over a large array of breeding lines. The relationship between short plants, short basal internodes and lodging resistance is well established (eg. Murthy and Rao 1980; Stapper and Fischer 1990; Keller et al. 1999). Both Dunn and Briggs (1989) and Stanca et al. (1979) reported that lodging resistance within small samples of barley cultivars (<10) was closely associated with both shorter plants with short basal internodes. Stanca et al. (1979) found no association between the number of vascular bundles, stem diameter, or culm wall thickness of the basal internodes and artificially induced lodging. They did find, among the two-row barley cultivars studied, that stiff-strawed cultivars had a higher number of vascular bundles than the weak-strawed cultivars, and they postulated that a high number of vascular bundles in combination with short basal internodes may confer lodging resistance (Stanca et al 1979). Dunn and Briggs (1989) suggested that lodging resistant barley genotypes exhibited a thicker culm wall and sclerenchyma ring in the second internode. They further suggested that the number of

vascular bundles was unstable over years and the number of internodes and culm diameter was not associated with the level of barley lodging resistance. Tandon et al. (1973), working with 62 barley genotypes, determined that plant height and culm wall thickness were important characters associated with lodging, but that basal internode length was relatively insignificant. In the 13 spring wheat genotypes we evaluated, plant height and the length of the basal internodes were also important traits to convey lodging resistance. No other measured culm character was important on a general scale, but as others reported, specific genotypes in this study did exhibit traits previously related to lodging resistance.

Mukherjee et al. (1980) evaluated 49 Indian wheat cultivars for the identification of morphological characters that could possibly be used as a basis for selection of lodging resistant material. They observed no association of plant height with actual field lodging, but did find that thicker stems were associated with less lodging (Mukherjee et al. 1980). Recently, Zuber et al. (1999) reported similar results from studying 15 Swiss wheat breeding lines. Plant height, the length of the basal internodes and the number of vascular bundles was not associated with lodging in that study. However, stem diameter explained almost half of the phenotypic variation in lodging resistance (Zuber et al. 1999). We did not find stem diameter to be a significant character related to lodging resistance.

Jellum (1962) studied 5 oat cultivars differing in lodging susceptibility, and reported the two lodging resistant cultivars had larger stem diameters and wider culm walls than the three lodging susceptible cultivars. The number of vascular bundles (found within the sclerenchyma, parenchyma and the total number), diameter of the lumen cavity, and width of the sclerenchyma layer showed no consistent relationship between lodging resistance and susceptible cultivars (Jellum 1962).

In the first year of the present study, we noticed that differences in the adventitious root system appeared to exist among the genotypes. The following year, plants were scored based on the number and size of adventitious roots emerging from the basal nodal regions. The lodging susceptible grouping exhibited a more extensive adventitious root system than the moderately tolerant grouping. These results are contrary to the findings Crook and Ennos (1994) reported in UK winter wheat. They found that because the short stiff culms of UK cultivars are able to resist bending or buckling, plants transmit the forces generated by wind action into the ground, causing the root system to rotate in the soil. They suggested that plants with stronger, more widely spread

adventitious roots may therefore be better able to resist external forces that cause lodging (Crook and Ennos 1994).

Without significant correlations with field lodging, and a high stability among cultivars and years, correlated plant characters will not be reliable indices for selection of lodging resistant material. A number of reasons may be attributed to a lack of significance among culm traits and lodging in the present study, and for other experiments cited above. Zuber et al. (1999) reported the growth stage at which sampling occurred, along with the quality of lodging data affect the strength of the correlation. In the present experiment, plants were sampled all at once, which is the most practical for a breeding program, yet this may imply that a range of growth stages was sampled, thereby confounding results.

The full yield potential of a given genotype under ideal growth conditions will not be realized without the ability to withstand lodging. The lack of general associations of culm anatomy characters, other than height, with lodging confirms the complex nature of this trait. Keller et al. (1999), while searching for quantitative trait loci (QTL) for lodging resistance discovered nine QTLs for lodging resistance, five of which coincided with QTLs for plant height. They therefore reported that plant height is probably the best morphological trait for the indirect selection for lodging resistance. We found no internal culm anatomy trait generally associated with lodging and thus they are of no interest for selective purposes within Canadian wheat breeding programs. The selection of shorter genotypes within the Canadian bread wheat germplasm should increase levels of lodging resistance. Nevertheless, no selection index or individual plant character can replace the assessment of lodging resistance in the field at multiple locations and years in the advanced stages of a breeding program (Pinthus 1973).

3.5 Summary

Selection for lodging resistant cultivars in cereal breeding programs is difficult due to the challenge of screening for this trait under natural field conditions. The identification of easily measurable culm traits related to lodging resistance would simplify the selection process. The present study was conducted to determine if differences in culm anatomy exist among modern wheat genotypes differing in lodging susceptibility, and to determine the association between culm characters and lodging. From a 2-yr field study conducted in Edmonton, AB, 13 spring wheat cultivars were chosen based on predetermined susceptibility to artificially induced lodging.

Morphological and anatomical culm measurements were made visually and with an environmental scanning electron microscope. Genotypes differed ($P < 0.05$) for plant height, number of internodes per culm, basal internode length and diameter, culm wall thickness and the number of vascular bundles, but not for adventitious root frequency, lumen diameter or sclerenchyma ring thickness. Mean genotype field scores for artificially induced lodging were correlated ($P < 0.05$) with plant height ($r = 0.51$) and the length of the 4th basal internode ($r = 0.51$). Short, wide basal internodes with thick culm walls and a high number of vascular bundles were characteristic of three lodging tolerant genotypes: Kohika, Sapphire and Olso. Despite such apparent genotype specific association between culm anatomy and field lodging, generally applicable associations were not observed for most traits. The most practical and easily selectable trait for lodging resistance within a wheat breeding program remains plant height.

3.6 Tables and Figures

Table 3.1. Origin, quality class, plant architecture and lodging resistance rating from published literature of 13 genotypes selected for a lodging experiment grown in Edmonton, AB (2000-2001).

Genotype	Origin[z]	Quality class[y]	Plant Architecture	Lodging rating[x] from literature
Kohika	NZ	Bread	Semidwarf	G
C9800L-048[w]	CIMMYT	HYV	Semidwarf	-
Oslo	NAPB	CPS-R	Semidwarf	EX
Sapphire	NZ	Bread	Semidwarf	EX
AC Foremost	SPARC	CPS-R	Semidwarf	EX
ND695	NDSU	CWRS	Semidwarf	EX
AC Domain	CRC	CWRS	Tall	VG
AC Intrepid	SPARC	CWRS	Tall	G
AC Vista	SPARC	CPS-W	Semidwarf	G
Laser	UA	CWES	Tall	EX
McKenzie	SWP	CWRS	Tall	F
AC Barrie	SPARC	CWRS	Tall	G
AC Splendor	CRC	CWRS	Tall	F

[z]NZ = New Zealand; CIMMYT = International Maize and Wheat Improvement Centre (Mexico); SPARC = Semiarid Prairie Agricultural Research Centre (Swift Current, Canada); NAPB = Nickerson American Plant Breeders Inc. (Colorado, USA); NDSU = North Dakota State University (ND, USA); CRC = Cereal Research Centre (Winnipeg, Canada); UA = University of Alberta (Edmonton, Canada); SWP = Saskatchewan Wheat Pool (Saskatoon, Canada).

[y]Bread = type in New Zealand; HYV = high yielding varieties; CPS – R, W = Canadian Prairie Spring – Red, White; CWRS = Canadian Western Red Spring.

[x]AAFRD 2002b; NZCFR 2000; MAES 2002; EX = excellent, VG = very good, G = good, F = fair.

Table 3.2. Natural and artificially induced lodging scores, plant height, number of internodes and presence of adventitious roots of 13 wheat genotypes grown in Edmonton, AB (2000-2001).

Genotype	Lodging susceptibility[z]	Natural lodging[y]	Artificial lodging[x]	Plant height (cm)	No. of internodes	Adventitious roots[w]
Kohika	T	1	2	73	5.0	0.7
C9800L-048	T	1	2	76	4.8	1.8
Oslo	T	1	2	80	5.3	2.4
Sapphire	T	1	3	81	4.7	2.7
T-grouping Mean		*1*	*2*	*77*	*5.0*	*1.9*
AC Foremost	M	1	4	79	5.3	1.4
ND695	M	2	5	88	5.0	1.7
AC Domain	M	2	6	100	5.3	0.9
AC Intrepid	M	2	6	103	4.9	1.3
M-grouping Mean		*2*	*5*	*93*	*5.1*	*1.3*
AC Vista	S	2	7	89	5.0	1.5
Laser	S	2	7	102	5.6	2.1
McKenzie	S	3	8	101	4.8	1.6
AC Barrie	S	2	8	104	5.1	2.5
AC Splendor	S	2	8	105	5.1	2.7
S-grouping Mean		*2*	*8*	*100*	*5.1*	*2.1*
F-tests						
Genotype		*	**	**	**	ns
Genotype*year		ns	*	*	ns	-
Contrasts						
T vs. M		ns	*	**	ns	ns
T vs. S		ns	**	**	ns	ns
M vs. S		ns	*	**	ns	*
SE[v]		0.36	0.75	2.0	0.16	0.69

ns, *, **: significant effects not significant ($P \geq 0.05$), or significant at $P < 0.05$ or 0.01, respectively.

[z] Based on mean rating following artificially induced lodging (T = lodging tolerant, M = moderately tolerant of artificially induced lodging, S = lodging susceptible).

[y] Lodging scored on a scale of 1 to 9 (1 = no lodging; 9 = total lodging).

[x] Artificial lodging induced at the early milk stage of the experiment.

[w] Scored on a scale of 0 to 5 (0 = no adventitious roots present; 5 = most developed root system), only in 2001.

[v] Standard error of the difference between two least-square means.

Table 3.3. Length and diameter of the four basal internodes[z] for 13 wheat genotypes grown in Edmonton, AB (2000-2001).

Genotype	Lodging susceptibility[y]	Internode length (cm)					Internode diameter (mm)				
		1st		2nd	3rd	4th	1st	2nd	3rd		4th
		2000	2001						2000	2001	
Kohika	T	2.2	2.1	6.0	9.7	15.2	2.57	3.26	3.52	3.72	3.53
C9800L-048	T	3.6	1.8	6.3	10.5	11.1	2.41	3.05	3.34	3.25	2.60
Oslo	T	3.8	2.1	5.4	8.2	12.2	2.28	2.99	3.37	3.26	3.09
Sapphire	T	4.6	2.7	7.7	11.7	12.0	3.04	3.59	4.05	3.77	2.85
T-grouping Mean		*3.6*	*2.2*	*6.3*	*10.0*	*12.6*	*2.57*	*3.22*	*3.57*	*3.50*	*3.02*
AC Foremost	M	4.3	1.8	6.4	9.5	16.6	2.47	3.19	3.29	3.70	3.66
ND695	M	3.4	2.8	7.9	13.3	17.5	2.52	3.10	3.29	3.76	3.04
AC Domain	M	2.7	2.6	7.6	13.3	20.8	2.12	2.80	2.83	3.19	3.01
AC Intrepid	M	5.0	2.9	9.1	17.3	18.2	2.50	3.17	3.06	3.58	2.61
M-grouping Mean		*3.8*	*2.5*	*7.8*	*13.3*	*18.3*	*2.40*	*3.07*	*3.12*	*3.56*	*3.08*
AC Vista	S	4.3	2.3	7.1	12.7	15.8	2.43	3.20	3.37	3.42	2.97
Laser	S	2.7	2.3	5.7	9.4	15.8	2.37	3.09	3.44	3.81	3.86
McKenzie	S	5.4	3.1	10.2	15.9	17.6	2.61	3.15	2.78	3.60	2.44
AC Barrie	S	3.2	2.6	9.8	15.7	23.2	2.48	3.23	2.91	3.66	3.12
AC Splendor	S	4.9	2.2	8.1	15.2	20.3	2.36	3.03	2.74	3.67	2.89
S-grouping Mean		*4.1*	*2.5*	*8.2*	*13.8*	*18.6*	*2.45*	*3.14*	*3.05*	*3.63*	*3.06*
F-test											
Genotype		**	*	**	**	**	**	*	*	*	*
Genotype*year			*	ns	ns	ns	ns	ns		**	ns
Contrasts											
T vs. M		ns	ns	*	*	*	ns	ns	*	ns	ns
T vs. S		ns	ns	*	*	*	ns	ns	*	ns	ns
M vs. S		ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
SE[x]		0.74	0.38	0.65	1.11	2.15	0.17	0.17	0.25	0.17	0.34

ns, *, **: significant effects not significant ($P \geq 0.05$), or significant at $P < 0.05$ or 0.01, respectively.

[z]Internodes numbered from the ground upwards.

[y]Based on preliminary experimentation (T = lodging tolerant, M = moderately tolerant to artificially induced lodging, S = lodging susceptible).

[x]Standard error of the difference between two least-square means.

Table 3.4. Culm wall thickness, lumen diameter and number of vascular bundles (either situated within the sclerenchyma ring or parenchyma tissue) of the second basal internode of 13 wheat genotypes grown in Edmonton, AB (2000-2001).

		No. of vascular bundles				Culm wall thickness	Lumen diameter	Sclerenchyma ring thickness
	Lodging	Sclerenchyma ring		Parenchyma	Total			
Genotype	susceptibility[z]	2000	2001			(mm)	(mm)	(μm)
Kohika	T	12	14	28	41	0.72	1.72	76.2
C9800L-048	T	9	11	29	39	0.74	1.63	71.3
Oslo	T	8	9	28	37	0.79	1.45	81.6
Sapphire	T	6	13	32	41	0.76	2.22	70.3
T-grouping Mean		*9a*	*12a*	*29a*	*40a*	*0.75a*	*1.75a*	*74.8a*
AC Foremost	M	10	11	32	42	0.69	1.94	72.2
ND695	M	10	13	25	36	0.67	1.77	67.2
AC Domain	M	11	12	26	38	0.58	1.75	67.0
AC Intrepid	M	13	11	28	40	0.74	1.64	67.2
M-grouping Mean		*11a*	*12a*	*28a*	*39a*	*0.67a*	*1.78a*	*68.3b*
AC Vista	S	10	11	30	41	0.64	1.85	61.7
Laser	S	11	9	28	38	0.78	1.65	76.6
McKenzie	S	9	9	27	36	0.60	1.94	71.4
AC Barrie	S	12	10	30	41	0.69	1.75	73.0
AC Splendor	S	11	14	27	39	0.73	1.47	77.1
S-grouping Mean		*10a*	*11a*	*28a*	*40a*	*0.69a*	*1.73a*	*72.0a*
F-test								
Genotype		**	**	*	*	*	ns	ns
Genotype*year			**	ns	ns	ns	ns	ns
SE[y]		1.4	0.9	1.7	1.8	0.05	0.19	6.02

ns, *, **: significant effects not significant ($P \geq 0.05$), or significant at $P < 0.05$ or 0.01, respectively.
[z]Based on preliminary experimentation (T = lodging tolerant, M = moderately tolerant to artificially induced lodging, S = lodging susceptible).
[y]Standard error of the difference between two least-square means.
*a-b*Means within columns with the same letter are not significantly different at P = 0.05, as determined from single degree of freedom contrasts.

Table 3.5. Spearman rank phenotypic and genotypic correlations[z] between plant height, internode number and length with natural and artificially induced lodging for 13 spring wheat genotypes grown in Edmonton, AB (2000-2001).

	Natural lodging		Artificially induced lodging	
Trait	Phenotypic	Genotypic	Phenotypic	Genotypic
Plant height	0.40	ns	0.46	0.51
Internode number	ns	ns	0.31	ns
1st internode length	ns	ns	ns	ns
2nd internode length	0.23	ns	ns	ns
3rd internode length	0.40	ns	0.29	ns
4th internode length	0.34	0.41	0.26	0.51

[z]All reported correlations significant at $P < 0.05$; ns indicates effects were not significant ($P \geq 0.05$). Correlations of adventitious root frequency, internode diameter, culm wall thickness, lumen diameter, number of vascular bundles, and thickness of sclerenchyma ring with lodging were not significant ($P \geq 0.05$) and are not presented.

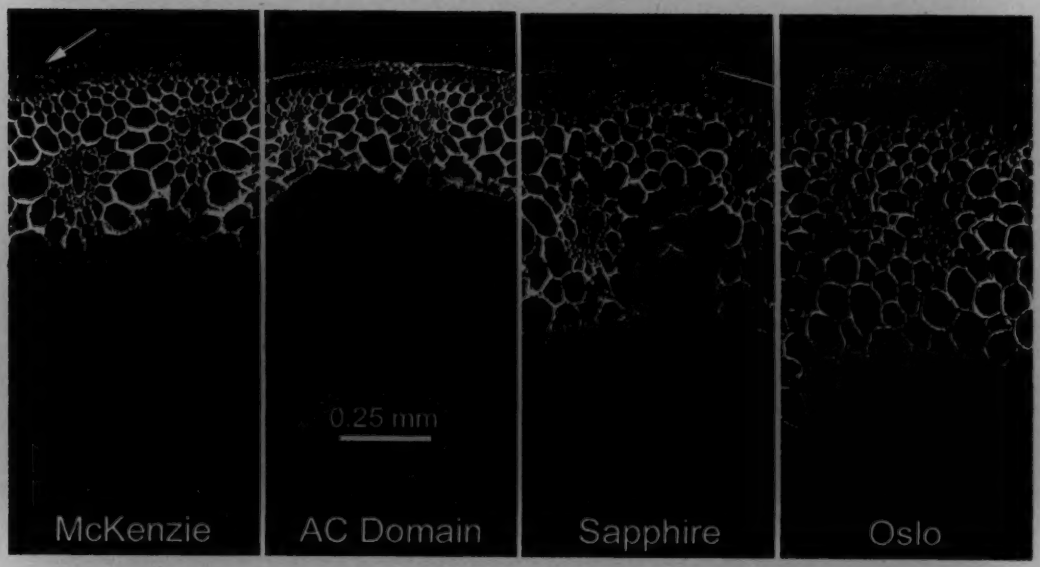

Figure 3.1. Differences in culm wall thickness, shown from a selected portion of the second culm internode cross section under an environmental scanning electron microscope, of four wheat genotypes differing in lodging susceptibility (ordered by increasing lodging tolerance from left to right). The arrow indicates the position of the sclerenchyma ring, just below the epidermis, with a vascular bundle embedded within.

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4.0 Agronomic evaluation of 24 spring wheat genotypes for a breeding program in the Parkland region of Alberta

4.1 Introduction

Canada is the world's largest exporter of hard red spring wheat (CWRS) and Canada is internationally known for consistently supplying uniform, high quality grain (Canadian Wheat Board 2003). The development of kernel visual distinguishability (KVD) and a century of breeding efforts are major factors contributing to the industry's success. Despite Canada's stringent grain quality requirements and climatic limitations, western Canadian wheat breeders have increased yield potential by 6-9 kg ha^{-1} yr^{-1} over the last 90 years (McCaig and DePauw 1994), while reducing days to maturity and elevating disease resistance. The most recently released CWRS cultivars have heavier kernels, and greater kernel number $spike^{-1}$ and spike-filling rate relative to older cultivars (Wang et al. 2002). Canadian wheat currently yields approximately 2.2 t ha^{-1}, on average (FAO 2003).

At the University of Alberta, the goal of the wheat breeding program is to develop early maturing bread wheat cultivars for a high yielding environment with a short growing season. Genotypes are typically evaluated for disease, heading, maturity, lodging, and grain yield. Recently, there is increased interest in organic grain production. Under such a system, plant height and tillering capacity are important traits in determining competitive ability.

Screening a wide range of spring wheat germplasm for lodging susceptibility (see Chapters 2 & 3) afforded us the opportunity to evaluate other agronomic traits that would not normally be collected in an advanced breeding trial. We evaluated numerous agronomic and yield component traits from a wide range of spring wheat genotypes varying in origin, quality class and plant architecture. Such information will be valuable when choosing genotypes for either cutlivar development or organic research at the University. The objectives of this chapter were: 1) to evaluate a wide range of spring wheat for numerous agronomic traits, 2) to determine each genotype's performance relative to the current western Canadian bread wheat check cultivar, AC Barrie and 3) to identify genotypes suitable to incorporate into the University of Alberta wheat breeding program.

4.2 Materials and methods

We conducted a 3-yr field experiment from 2000-2002 at the Edmonton Research Station, Edmonton, Alberta (53° 34' N, 113° 31' W). The experiment was planted as a split plot arrangement of a randomized complete block design with four blocks. Wheat genotypes were planted to the main plots and seeding rates to the subplots. Twenty-five wheat genotypes (both cultivars and breeding lines) were included, representing a variety of origins, quality classes and plant architecture (see Chapter 2; Table 2.2). The Canadian extra strong cultivar Laser was thereafter dropped from the analysis as it was the only extra-strong genotype in the study. Seeding rate treatments for the present study included a local recommended seeding rate of 250 seeds m^{-2} and a doubled seeding rate. Crop husbandry for the experiment has been described earlier (Chapter 2).

Following stem elongation, plant height was recorded from the soil surface to the tip of the spike, excluding awns, from both seeding rates. Disease severity was estimated visually on each plot at anthesis, with a score of 1 (none) to 9 (entire canopy infected) assigned for each disease. Septoria tritici blotch (*Septoria triciti*) and powdery mildew (*Erysiphe graminis)* were present in 2000 and 2001, with no disease present in 2002. Heading date was recorded when 50% of spikes completely emerged and maturity was estimated when plots were visually 75% ripe, by squeezing the grain to determine hardness. Both heading and maturity are presented as days after seeding. Spikes m^{-2} were determined from a 1-m row sample randomly selected in either the first or fourth row of each plot. At maturity, the same 1-m row sample was hand sickled at ground level for the determination of harvest index, calculated as the ratio of grain weight to total plant weight (grain + straw). Prior to harvest, ten spikes per plot were randomly collected from each plot for kernel number $spike^{-1}$ and kernel weight calculation. In 2000, plots were trimmed back to 5-m and the middle two rows were hand harvested with a sickle as each plot matured, bagged, dried at 60°C and threshed by a stationary thresher. In subsequent years, a plot combine harvested the entire 4 row x 6 m plot for yield, which was determined after the sample was cleaned and dried. Test weight was determined from a 550-ml subsample. Vandalism in early September 2000 resulted in the loss of one block for that year. Spikes m^{-2}, kernel number $spike^{-1}$ and harvest index were not recorded in 2000.

Grain protein was determined from near infrared (NIR) spectroscopy by on recommended seeding rate treatment samples only, calibrated with wet-lab samples from the Grain Research Laboratory (Winnipeg, MB). Clean, whole grain samples were scanned using a

monochromator NIRSystems model 6500 (Foss NIRSystems, Inc., Silver Springs, MD, U.S.A) at the Cereal Unit of AAFRD in Lacombe, AB. The reflectance spectrum of 400 – 2500 nm was recorded at 2 nm intervals for each sample.

Data were analyzed within mixed models (both random and fixed effects) using the Proc MIXED procedure of SAS, employing the Kenward Roger option to specify the method in computing denominator degrees of freedom for testing of fixed effects and calculating least-square means (Littell et al. 1996). Year, block and associated interactions were considered random effects, and seeding date, genotypes and seeding date × genotypes were considered fixed effects. The MIXED procedure accounts for both intra and inter-year and block variation. Within such analysis interactions between year and genotype are not tested, as they are considered random. This allows for a generalized interpretation of genotype/cultivar performance over many years while adjusting for heterogeneous error variances. PROC GLM was employed to test the interaction of seeding date × genotype with the appropriate error term of year × seeding date × genotype.

Fixed effect differences are discussed only when $P < 0.05$. Least-square means and standard error of the difference between two least-square means is presented throughout (Steel et al. 1997). Valid estimates of heritability can only be made on randomly selected genotypes within a population. Fehr (1987) suggested that the term "repeatability" be used to describe the ratio of genotypic variation to phenotypic variation in a non-randomly selected group of genotypes. Measures of broad-sense repeatability for each agronomic trait over the 3 years were calculated, using variance estimates derived from the MIXED procedure of SAS, as the ratio of genotype variance to the sum of genotype, year × genotype, seeding date × genotype, year × seeding date × genotype and error variances (Fehr 1987). AC Barrie (McCaig et al. 1996) was used as the check cultivar.

4.3 Results

Seeding rate × genotype interactions were not significant for all traits, except spikes m^{-2}. All traits except spike m^{-2} were thereafter combined over the 2 seeding rates and 3 years data (Table 4.1). Due to the complex nature of the seeding rate × genotype interaction for spike m^{-2}, the analysis for this trait was thereafter conducted and presented for the recommended seeding rate only. From yearly mean values, it is evident the lack of precipitation affected all traits in 2002. On average, genotypes yielded approximately 40% of the previous 2-yr means (Table 4.1). In comparison to 2001, genotypes produced 110 less spike m^{-2} and 12 less kernels $spike^{-1}$ that were 2 mg lighter. Average test weight increased by 3 kg hL^{-1} and grain protein percent increased 1.1%, respectively. On average, genotypes headed and matured 5 and 13 days earlier, respectively. Plants were 30 cm shorter and harvest index increased by 6 percentage points in 2002 compared to 2001.

In combined-year analysis, genotypes differed ($P < 0.05$) for all eleven agronomic traits (Table 4.1). Genotypes ranged in mean grain yield from 3.03 to 5.14 t ha^{-1}, with Canadian western red spring (CWRS) breeding lines yielding low and New Zealand and US bread genotypes yielding high, on average. Compared to AC Barrie, 9007-FB01C yielded 10% lower, whereas Sapphire yielded 53% more (Table 4.2). All other bread wheats from New Zealand and US, and Canadian prairie spring (CPS) and CIMMYT genotypes out yielded AC Barrie by 30%, with the exception of Otane (23%) and C9800L-048 (27%).

Genotypes ranged by 9 and 15 days for heading and maturity, respectively (Table 4.1). Oslo was the earliest to head and was second earliest, to that of AC Splendor, to mature. Sapphire, a New Zealand bread wheat, was the latest of all genotypes to head and mature. Relative to AC Barrie, all other CWRS cultivars headed and matured earlier (Table 4.2). Little variation within CWRS breeding lines existed for days to heading and 6 of 7 lines matured later than AC Barrie. Oslo and C9800L-048 were the only other genotypes within the experiment to head and mature earlier than AC Barrie. Some bread wheat genotypes from New Zealand and US were a day earlier to head than AC Barrie, but all other genotypes matured after AC Barrie, with Sapphire, N93-0119 and ND695 reaching maturing more than a week later.

From the 3-yr average, genotypes varied by 27 cm for plant height. Two genotypes were taller than 90 cm (9007-FH01C2 and 9007-FH01D3) and 3 genotypes were shorter than 70 cm (Kohika, C9800L-015 and C9800L-048) (Table 4.1). Many of the CWRS genotypes were of

similar height to AC Barrie, but 2 breeding lines (9207-DB3*D and 9207-DB3*E2) were 10 cm shorter. Kohika was 23% shorter than AC Barrie, with the majority of genotypes from New Zealand, US and CIMMYT shorter by 15% or more.

Leaf disease infection was not severe in all 3 study years, with no disease present in 2002. Infections of powdery mildew were only observed in AC Barrie in 2000 and 2001 (data not shown). Genotypes differed from infection severity of Septoria tritici blotch, ranging between 2-5 in severity score. Genotypes of New Zealand and CIMMYT origin were most severely infected and genotypes of US origin exhibited higher levels of resistance than all Canadian genotypes.

The number of spikes m^{-2} ranged from 285 (Kohika) to 495 (N93-0119) for the 24 genotypes examined (Table 4.1). US genotypes were among the highest tillering, while New Zealand genotypes were among the lowest tillering. All CPS genotypes tillered lower than the overall average of 400 spikes m^{-2}. The number of spikes m^{-2} between the CWRS cultivars differed, with AC Splendor tillering less than AC Barrie, and AC Domain and McKenzie tillering more than AC Barrie.

Genotypes ranged from 24 to 49 kernels $spike^{-1}$ (Table 4.1). All CWRS genotypes had 30 or less kernels $spike^{-1}$, with most breeding lines exhibiting less kernels $spike^{-1}$ than AC Barrie (Table 4.2). Three of the 4 New Zealand genotypes had more than 35 kernels $spike^{-1}$, with Sapphire having 49 kernels $spike^{-1}$.

With a mean of 36 mg for kernel weight, genotypes ranged by 13 mg (Table 4.1). The kernel weight of CWRS breeding lines varied, with kernels of 9007-FH01C 5 mg lighter than AC Barrie and kernels of 9207-DB3*D 5 mg heavier than AC Barrie (Table 4.2). Kernels from CPS and New Zealand genotypes were heavier, while genotypes of CIMMYT origin were unchanged from AC Barrie.

All genotypes exhibited a test weight within the range of 76-79 kg hL^{-1}, with the exception of AC Splendor and Sapphire which had test weights of 75 and 74 kg hL^{-1}, respectively (Table 4.1). Genotypes ranged by 3.5 percentage points for grain protein, with an overall mean of 14.2%. Sapphire and C9800L-048 had the lowest protein content (12.6%), while 9007-FH01C2 grain had high protein (16.2%). All CWRS genotypes, with the exception of AC Intrepid, had high protein, with 4 of the 7 CWRS breeding lines having 8% or higher protein content than AC Barrie. The bread wheat genotypes of New Zealand and US origin and CPS genotypes all had less protein than AC Barrie.

Genotypes ranged by 15 percentage points for harvest index, with 9007-FH01C2 having the lowest harvest index (HI) of 38% and Otane having the highest HI of 53% (Table 4.1). All CWRS breeding lines had lower HI than AC Barrie, with the exception of 2 genotypes (9207-DB3*D and 9207-DB3*E2) that were approximately 10% higher. Bread wheat genotypes of New Zealand and US origin and CPS genotypes all had HI higher than AC Barrie by 10%.

Most repeatability estimates were moderate to high (Table 4.1). The low repeatability estimate for test weight (22%) indicates genotypic variation was small in relation to environmental variation, whereas a high estimate for heading date (74%) indicates a high proportion of observed variation was from genotypic differences.

4.4 Discussion and conclusions

On average, Canadian wheat currently yields 0.5 t ha^{-1} less than reported global averages (FAO 2003). The yield potential of western Canadian germplasm is limited by the short growing season, relatively low precipitation and the grain quality requirements of CWRS. Strict seed shape and size requirement constrains rapid genetic improvement and reports estimate a 5% loss in yield potential has been sacrificed to maintain KVD over the years (DePauw et al. 1995). The benchmark standard for grain protein concentration has restricted the incorporation of dwarfing genes into Canadian bread wheat germplasm. Along with reduced plant height, dwarfing genes exert the beneficial pleiotropic effect of improved spikelet fertility, increasing the number of kernels $spike^{-1}$ and grain yield potential (Gale and Youssefian 1985). On the other hand, adherence to these quality standards may have resulted in increased sales and/or possibly higher prices for Canadian wheat producers. Until another means of segregation can be widely implemented, any lenience of these requirements may compromise Canada's reputation of consistently delivering uniform, high-quality classes of wheat (Canadian Grain Commission 2003).

The 24 genotypes evaluated in this study exhibited a wide range of results for all traits, with the exceptions of leaf spot diseases and test weight. The characteristic traits of Canadian bread wheat are clearly displayed in this study. CWRS genotypes were early maturing, tall, and relatively low yielding, with high protein content. All semidwarfs entries had higher kernel number $spike^{-1}$ and genotypes of CPS, New Zealand, and CIMMYT origin all out-yielded CWRS genotypes, but at the expense of grain protein. McClung et al. (1986) reported a strong association between plant height and grain protein concentration in durum wheat ($r = 0.80$, $P <$

0.01) and noted factors in addition to the dilution of grain protein from high yield are responsible for the low grain protein concentration associated with semidwarfs. US wheat genotypes had low disease infection scores and had comparable protein levels to CWRS, but matured a week later than the check cultivar.

Harvest index data is usually not determined in breeding trials due to the work required. A higher harvest index is an expression of greater plant efficiency since a greater proportion of the available assimilates is being translocated into the grain. CWRS class exhibited low harvest indexes, with no genotype surpassing 50%. The selection for shorter, high yielding varieties (mainly containing dwarfing genes) are generating harvest indexes exceeding 50% in genotypes worldwide (Austin et al. 1980).

Hucl and Baker (1987) studied ancestral and modern Canadian spring wheat cultivars and determined plant height, harvest index and grain yield have not undergone consistent improvements since the release of Thatcher (1934), with the number of kernels spike^{-1}, grain yield spike^{-1} and test weight unchanged since Marquis (1909). Genetic yield gains over time in CWRS have been generally attributed to increases in kernel weight (Hucl and Baker 1987). Wang et al. 2002 evaluated four 'new' CWRS cultivars (oldest released in 1994) in comparison to 2 older CWRS cultivars. The average yield of the newer cultivars exceeded Neepawa (released in 1969) by only 6% and Marquis (released in 1909) by 34%. However, these new cultivars had increased kernel weight, kernels spike^{-1} and spike filling rate (calculated by dividing the yield spike^{-1} by the grain filling rate, the time between anthesis and physiological maturity). The number of spikes plant^{-1} and the length of the grain-filling period do not appear to the associated with increased yield (Wang et al. 2002). Hucl and Baker (1987) postulated the strong association between grain yield and time to spike emergence has limited improvements in CWRS. They suggest future improvements in grain yield might result from selection for higher harvest index since it is related to grain yield ($r = 0.63$) but not maturity (Hucl and Baker 1987).

Two CWRS breeding lines (9207-DB3*D and 9207-DB3*E2) show potential to decrease plant height, improve yield and increase harvest index without jeopardizing grain quality. To abide with KVD standards of kernel shape and size, little opportunity may exist to further increase kernel weight in CWRS germplasm. The higher kernel weight of these 2 genotypes may require further selection. Additional sources of short height, high tillering, and high kernels spike^{-1} exist to increase grain yield and harvest index of CWRS. However, the efforts required to attain reasonable maturity and to select Canadian grain quality may be great.

Calculated repeatability estimates of most traits should result in breeding gains from selection. Days to heading and maturity, and plant height were highly heritable traits, requiring less replicated evaluation compared to disease susceptibility or yield. Poehlman and Sleper (1995) indicated among the yield components, kernel weight tends to have the highest heritability coefficient. This was confirmed in this study, with little observed variation in spike m^{-2} and kernel $spike^{-1}$ attributed to genotypic differences. McKendry et al. (1988), studied the inheritance of grain protein concentration, grain yield and related traits in spring wheat crosses made in Winnipeg and reported similar broad sense heritabilities for protein (57–76%) and harvest index (49-58%). Their estimates for grain yield (51-70%) were, however, higher than calculated in this study (McKendry et al. 1988). Heading, maturity and plant height repeatability estimates were in agreement with Wong and Baker (1986), researchers from Saskatoon who investigated numerous methods to measure time to maturity in spring wheat. Baker et al. (1971), studying heritabilities and correlations among quality traits in Canadian wheat, also determined a high estimate for grain protein (80%), but an extremely high estimate for test weight (89%) that was not found in this study.

Selected genotypes at either extreme for each trait are listed in Table 4.3 for convenient reference. Wide ranges of spring wheat germplasm are readily available at the University of Alberta for breeding and experimental purposes. For example, the high tillering nature of the tall CWRS cultivar McKenzie may be of interest for organic research. In addition to the CWRS breeding lines 9207-DB3*D and 9207-DB3*E2, particular genotypes of New Zealand, US and CIMMYT origin may offer sources of high yield, early maturity, short stature and reasonable protein content for CWRS cultivar development. The 2 US genotypes (N93-0119 and ND695) have comparable protein content, with high yield and high leaf disease resistance, but are late to mature. The New Zealand cultivar, Kohika, matures only 1 day later than AC Barrie, has high grain yield with high kernel number $spike^{-1}$ and is short. Unlike Kohika, the protein content of 4837.04 (New Zealand origin) is approaching AC Barrie, and also has high kernel number $spike^{-1}$, is short and matures between AC Vista and AC Foremost. However, the disease susceptibility of these 2 New Zealand genotypes may limit their yield potential in western Canada. The short genotypes originating from CIMMYT are sources of high grain yield and early maturity, but have also shown disease susceptibility.

4.5 Tables

Table 4.1. Least square means for 24 spring wheat genotypes (varying in origin and quality class) for eleven agronomic traits evaluated at a local recommended & double seeding rate and repeatability estimates from a 3-yr field experiment grown at Edmonton, AB (2000-2002).

Genotype	Origin & quality class[a]	Grain yield (t ha^{-1})	Heading (days)	Maturity (days)	Plant height (cm)	Leaf spot (1-9)	[x]Spike m^{-2} (no.)	Kernels spike^{-1} (no.)	Kernel weight (mg)	Test weight (kg hL^{-1})	[x]Protein (%)	Harvest index (%)
AC Barrie		3.36	60	109	89	4	405	29	35	77	14.6	44
AC Domain		3.66	58	107	84	3	470	26	35	77	14.9	45
AC Splendor	*CWRS*	3.39	57	105	89	3	355	29	35	75	15.2	44
AC Intrepid		3.60	57	107	89	3	420	28	37	76	14.5	46
McKenzie		3.46	57	107	89	4	475	28	32	76	14.7	44
9007-FB01C		3.03	62	113	83	4	450	27	30	77	15.5	40
9007-FH01C2		3.36	60	112	91	3	380	28	37	78	16.2	38
9007-FH01C4	*CWRS*	3.56	58	111	90	3	395	26	35	78	15.7	40
9007-FH01D3	*breeding*	3.13	60	111	93	3	420	26	35	78	16.1	39
9107-BT04B	*lines*	3.26	60	108	91	4	395	24	39	76	15.8	43
9207-DB3*D		3.79	61	112	79	3	385	27	40	79	14.7	47
9207-DB3*E2		3.97	59	110	79	4	415	30	38	78	14.7	47
Oslo		4.30	56	106	72	3	370	32	36	77	13.0	50
AC Foremost	*CPS*	4.46	60	115	71	4	350	34	41	77	13.0	50
AC Vista		4.44	60	113	81	3	355	33	43	76	13.0	50
AC 2000		4.52	63	114	80	4	355	35	42	77	13.1	46
Sapphire	*New*	5.14	65	120	75	3	285	49	41	74	12.6	51
Otane	*Zealand -*	4.13	62	114	70	5	300	36	40	77	12.8	53
Kohika	*bread*	4.54	59	110	66	5	355	36	39	78	12.9	52
4837.04		4.59	62	114	73	3	400	32	39	78	13.8	48
N93-0119	*US -*	4.63	59	116	72	2	495	33	37	78	14.5	50
ND695	*bread*	4.57	59	118	78	2	470	32	38	79	14.3	50
C9800L-015	*CIMMYT*	4.80	59	108	69	3	420	32	35	79	13.4	48
C9800L-048		4.27	57	107	68	5	400	33	35	77	12.6	48
Mean$_{2000}$		5.23	62	117	98	4	-	-	36	75	13.6	-
Mean$_{2001}$		4.78	61	115	86	3	450	37	39	77	13.9	43
Mean$_{2002}$		1.98	56	102	56	-	341	25	37	80	15.0	49
Mean$_{overall}$		4.00	60	111	80	4	400	31	36	77	14.2	46
Genotype *F*-test		**	**	**	**	**	*	*	**	**	**	**
Genotype × seeding rate *F*-test		ns	ns	ns	ns	ns	**	ns	ns	ns	-	ns
Repeatability estimate (%)		42	74	70	62	33	25	34	57	22	70	44
SE[y]		0.35	0.8	1.4	4.7	0.5	43	4.4	1.6	1.1	0.53	0.03

ns, *, **: not significant ($P \geq 0.05$) and effects significant at $P < 0.05$ and 0.01, respectively.

[x]Not combined over seeding rates, recommended seeding rate only.

[y]Standard error of the difference between two least-square means.

[a]CWRS = Canadian western red spring, CPS = Canadian prairie spring.

Table 4.2. Combined-year analysis of agronomic performance of 23 spring wheat genotypes relative to AC Barrie at Edmonton, AB (2000-2002).

Genotype	Origin & quality class	Relative to AC Barrie: Grain yield (%)	Heading (days)	Maturity (days)	Plant height (cm)	[z,y]Spike m^{-2} (no.)	[z]Kernels $spike^{-1}$ (no.)	Kernel weight (mg)	Test weight (kg hL^{-1})	[y]Protein (%)	[z]Harvest index (%)
AC Barrie		*100*	*60*	*109*	*89*	*405*	*29*	*35*	*77*	*14.6*	*100*
AC Domain	*Canadian CWRS*	109	-2	-2	-5	65	-2	-1	0	0.3	104
AC Splendor		101	-4	-4	0	-50	0	0	-2	0.6	101
AC Intrepid		107	-3	-2	0	15	0	2	-1	-0.1	107
McKenzie		103	-3	-2	0	70	-1	-4	-1	0.1	102
9007-FB01C	*Canadian CWRS breeding lines*	90	2	4	-6	45	-1	-5	0	0.9	93
9007-FH01C2		100	0	3	2	-25	-1	2	1	1.6	89
9007-FH01C4		106	-2	2	1	-10	-2	0	1	1.1	93
9007-FH01D3		93	0	2	4	15	-2	-1	1	1.5	91
9107-BT04B		97	0	-1	2	-10	-5	4	-1	1.2	99
9207-DB3*D		113	1	3	-10	-20	-2	5	1	0.1	109
9207-DB3*E2		118	-1	1	-10	10	1	3	0	0.1	108
Oslo	*Canadian CPS*	128	-4	-3	-17	-35	3	1	0	-1.6	116
AC Foremost		133	0	6	-18	-55	5	6	0	-1.6	116
AC Vista		132	0	4	-8	-50	4	8	-1	-1.6	116
AC 2000		135	3	5	-9	-50	6	7	0	-1.5	107
Sapphire	*New Zealand - bread*	153	5	11	-14	-120	20	6	-3	-2.0	118
Otane		123	2	5	-19	-105	7	5	0	-1.8	122
Kohika		135	-1	1	-23	-50	7	4	0	-1.7	121
4837.04		137	2	5	-16	-5	4	4	0	-0.8	111
N93-0119	*US - bread*	138	-1	7	-17	90	4	2	1	-0.1	116
ND695		136	-1	9	-11	65	3	3	1	-0.3	115
C9800L-015	*CIMMYT*	143	-1	-1	-20	15	3	0	1	-1.2	111
C9800L-048		127	-3	-2	-21	-5	4	0	0	-2.0	111

A negative value indicates the value was lower than that of AC Barrie.

[z]Missing 2000 data.

[y]Not combined over seeding rates; recommended seeding rate (250 seeds m^{-2}) only.

Table 4.3. Selected spring wheat genotypes differing for eleven agronomic traits in Edmonton, AB (2000-2002).

Trait	Grain yield	Heading	Maturity	Plant height	Leaf spot	Spikes m^{-2}	Kernels $spike^{-1}$	Kernel weight	Test weight	Grain protein	Harvest index
	Sapphire	Oslo	AC Splendor	Kohika	N93-0119	N93-0119	Sapphire	AC Vista	9207-DB3*D	9007-FH01C2	Otane
High,	C9800L-015	AC Splendor	Oslo	C9800L-048	ND695	McKenzie	Otane	AC 2000	C9800L-015	9007-FH01D3	Kohika
early or	N93-0119	C9800L-048	AC Intrepid	C9800L-015	AC Domain	AC Domain	Kohika	Sapphire	ND695	9107-BT04B	Sapphire
short	4837.04	McKenzie	C9800L-048	Otane	AC Splendor	ND695	AC 2000	AC Foremost	9007-FH01C4	9007-FH01C4	Oslo
	ND695	AC Intrepid	McKenzie	AC Foremost	AC Intrepid	9007-FB01C	AC Foremost	Otane	N93-0119	9007-FB01C	AC Foremost
	9007-FH01C2	Otane	Otane	McKenzie	AC Foremost	AC 2000	9207-DB3*D	AC Splendor	9107-BT04B	AC Vista	9107-BT04B
Low,	AC Barrie	4837.04	AC Foremost	9007-FH01C4	AC 2000	Kohika	9007-FH01C4	9007-FH01D3	McKenzie	Kohika	9007-FH01C4
late or	9107-BT04B	9007-FB01C	N93-0119	9007-FH01C2	Otane	AC Foremost	9007-FH01D3	AC Domain	AC Vista	Otane	9007-FB01C
tall	9007-FH01D3	AC 2000	ND695	9107-BT04B	Kohika	Otane	AC Domain	McKenzie	AC Splendor	Sapphire	9007-FH01D3
	9007-FB01C	Sapphire	Sapphire	9007-FH01D3	C9800L-048	Sapphire	9107-BT04B	9007-FB01C	Sapphire	C9800L-048	9007-FH01C2

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5.0 General discussion and conclusions

The development of lodging resistant cultivars has been a long-standing objective of cereal breeders worldwide. Lodging contributes to economic losses from reduced grain yield and quality, and harvest efficiency and down-grading of the harvested crop.

Significant improvements in genetic lodging resistance has resulted from a reduction in plant height, with average plant height reduced from 150 cm to 85 cm over the past 150 years of wheat breeding (Worland and Snape 2000). The discovery and incorporation of *Rht* genes has allowed breeders to reduce plant height, while increasing yield potential.

With the majority of global wheat germplasm of semidwarf stature, the risk of lodging has been diminished significantly. In reviewing the literature, most lodging research was conducted over 40 years ago. Crook and Ennos (1993) reported that stem lodging is relatively uncommon in modern UK wheat crops, as breeders have selected for shorter, more rigid stems over the past number of decades. Of the new literature published, most has been conducted in the UK under moist soil conditions where plants lodge primarily from weakly anchored roots.

Rht genes have not been incorporated into CWRS cultivars. The substantial increase in yield potential conferred through dwarfing genes dilutes protein content, rendering potential semidwarf lines unacceptable for CWRS quality. Although not a significant global producer in terms of quantity, Canada has a reputation for supplying high quality, high protein bread wheat.

Plant height of Canadian bread wheat has not changed greatly since 1934 (Hucl and Baker 1987). With suitable genetic variation existing to increase yield potential, western Canadian wheat breeders have identified stem-lodging resistance as an important breeding priority over the next several years (Western Grains Research Foundation, 1995).

Sources of strong straw strength need to be identified to increase genetic lodging resistance. Given the random appearance of weather events that induce lodging, natural field lodging assessments may not provide information regarding any given genotype's true potential to lodge. Developing a more repeatable method of selection formed the basis of this thesis, with the following objectives:

1) To determine a suitable, efficient method to screen for lodging susceptibility in wheat
2) To evaluate lodging susceptibility in Canadian and other spring wheat germplasm
3) To evaluate the effect of lodging on grain yield and quality
4) To determine whether lodging tolerant and susceptible genotype differ in culm anatomy and whether any differences are associated with lodging that could be used as a selection tool
5) To determine whether an environmental scanning electron microscope (ESEM) is an efficient method to screen for internal culm characters
6) The evaluate spring wheat genotypes for their incorporation into the western Canadian hard red spring wheat breeding program to improve genetic lodging resistance.

The following are summary points from each of the 3 chapters developed from these objectives:

Assessing lodging susceptibility in spring wheat breeding programs

- Little natural lodging occurred during 3 study years (even under a doubled seeding rate), making it extremely difficult to differentiate lodging susceptibility among genotypes under naturally occurring lodging
- Artificially inducing lodging by pulling a weighted plywood apparatus lengthwise across a 4 row, 6 m plot at the early milk stage was effective to screen and identify lodging tolerant and susceptible genotypes in the two years of study. However, under severe drought conditions (2002), this artificial lodging technique was unable to differentiate between genotypes. Even under a severe lodging treatment, the occurrence and/or severity of a lodging is dependent upon climatic conditions of the growing season.
- Lodging scores of natural and artificially induced lodging, and the two application times to artificially induce lodging were associated and therefore applying artificial lodging at the early milk stage of the experimental mean allows for the assessment of lodging susceptibility in an efficient, repeatable, practical manner
- Most CWRS genotypes were unable to resist or recover from artificially induced lodging

- Sources of lodging tolerance were identified, most of which were semidwarfs. Some exhibited the ability to resist artificially induced lodging, while others were able to recover.
- The 5 most lodging tolerant spring wheat genotypes (with plant height) were: 4838.04 (82 cm), Kohika (73 cm), C9800L-048 (76 cm), Oslo (83) and Otane (79 cm)
- The 5 most lodging susceptible spring wheat genotypes (with plant height) were: 9007-FH01D3 (110 cm), 9007-FH01C4 (105 cm), 9007-FH0C2 (108 cm), AC Splendor (104 cm) and 9107-BT04B (107 cm).
- Lodging was strongly associated with plant height over the two study years ($r = 0.58$).
- Lodging was negatively associated with yield ($r = -0.90$), with average losses in kernel number spike^{-1}, kernel weight, test weight, and grain yield of 5%, 11%, 4% and 26%, respectively, which translates with a reduction of 2 kernels spike^{-1}, 4 mg kernel^{-1}, 3 kg hL^{-1} in test weight, and 1.28 t ha^{-1} of grain yield.

The association of culm anatomy with lodging susceptibility in modern spring wheat genotypes

- Genotypes differed for plant height, number of internodes per culm, basal internode length and diameter, culm wall thickness and the number of vascular bundles, but not for adventitious roots, lumen diameter or sclerenchyma ring thickness.
- As a group, lodging tolerant genotypes had shorter basal internodes and a thicker sclerenchyma ring
- An environmental scanning electron microscope is an efficient method to observe and measure internal culm traits
- Short plants with more short, wide basal internodes with thick culm walls and a high number of vascular bundles were characteristic of some lodging tolerant genotypes
- Plant height was the only trait strongly associated with lodging tolerance
- Although genotype specific associations between culm anatomy and field lodging were apparent, generally applicable associations were not observed for most traits
- The most practical and easily selectable trait for lodging resistance within a spring wheat breeding program is plant height

Agronomic evaluation of 24 spring wheat genotypes for a breeding program in the Parkland region of Alberta

- Variability exists to improve grain yield, plant height, kernel number spike^{-1}, kernel weight, protein and harvest index
- Improvements should occur from selection for early heading and maturity, plant height, kernel weight and protein, as they exhibited high repeatability estimates
- The following cultivars ranked at either extremes for the listed traits:

Agronomic trait	High, early, short or resistant	Low, late, tall or susceptible
Grain yield	Sapphire	9007-FB01C
Heading	Olso	Sapphire
Maturity	AC Splendor	Sapphire
Plant height	Kohika	9007-FH01D3
Leaf spot	N93-0119	C9800L-048
Spikes m^{-2}	N93-0019	Sapphire
Kernels spike^{-1}	Sapphire	9107-BT04B
Kernel weight	AC Vista	9007-FB01C
Test weight	9207-DB3*D	Sapphire
Grain protein	9007-FH01C2	C9880L-048
Harvest index	Otane	9007-FH01C2

Altering agronomic management practices, cultivar blending or the use of plant growth regulators are options to prevent lodging, but may not be feasible in Canadian agriculture, due to climatic, quality and economic limitations. Ultimately, the development of resistant cultivars is the most cost-effective, sustainable and long-term solution.

From the artificial lodging technique adopted from Briggs (1990), improved lodging data and descriptions are now available to depict lodging susceptibility in CWRS wheat. It appears CWRS cultivars may be prone to lodging under conducive conditions, resulting in yield losses as high as 42%. Although not a current problem in CWRS production, initiating the breeding process today will be a prudent approach to minimize any future potential economic losses to the Canadian producer and consumer.

The use of this artificial lodging technique requires a considerable amount of seed. Preliminary work with hill plots, single rows of 2 and 6 m length was unsuccessful in inducing artificial lodging, as large 'edge effects' did not allow lodging to occur and one was not able to differentiate between genotypes (K. Briggs, personal communication). The conclusion of this

preliminary work led us to work within 4-row, 6 m long plots with the described lodging apparatus to screen for lodging susceptibility.

From the results of this thesis, we suggest that during early generations, one should select for short plant height. When enough seed is available (most likely F_7, preliminary yield trail stage), one may artificially induce lodging in the back block of a given trial at the early milk growth stage. Only one or two blocks would need to be screened due to the high repeatability of the test. One may choose to score immediately following the artificial lodging treatment and at harvest to determine the ability to recover from lodging. However, scoring immediately after the treatment will be sufficient to differentiate genotypes. The seed may not be lost if required for the next generation, as we were able to retrieve all the seed in our experiment (although germination tests were not done). This screening technique should give a relative ranking of the genotypes, indicating their lodging susceptibility.

With this screening technique, sources of lodging tolerance have been identified from this study. The agronomic evaluation indicates incorporation of many lodging tolerant sources may require backcrossing and selection to achieve desirable grain quality, disease resistance and earliness required for the Parkland region. However, the CWRS breeding lines within the 9207-DB3 series exhibit lodging tolerance, while possessing all other suitable agronomic traits. 9207-DB3*D and 9207-DB3*E2 are advanced breeding lines from crosses of AC Domain and Grandin, a US hard red spring wheat with *Rht1* gene (R. Depauw, personal communication). Both are moderately tolerant to artificially induced lodging (average score of 5 for both), are 10 cm shorter and yielded 15% higher than AC Barrie, on average. Although they mature later than AC Barrie, 9207-DB3*D and 9207-DB3*E2 maintain check protein content, and exhibit an improved harvest index.

Agriculture Canada has taken the next breeding step and has crossed lodging tolerant genotypes (4837.04 and C9800L-015) with elite CWRS genotypes (AC Barrie, AC Domain, and AC Splendor). These crosses are currently in the F_7 generation (single seed descent derived) and were grown in Edmonton this year in hill plots. Selection was made for maturity, plant height and disease resistance. Testing will continue for grain yield and quality with the ultimate goal to develop a CWRS cultivar for the Parkland regions of the prairies.

Since this project started, Agriculture and AgriFood Canada has registered a CWRS from a cross of AC Domain and Grandin that meets CWRS quality requirements and is a semidwarf. In 2000, AC Superb was released for commercial use. This variety has high yield potential from

the US parent and meets the CWRS grain quality requirements. In the Edmonton region, AC Superb out-yielded Katepwa by 20% and AC Barrie by 19%. AC Superb is a day later than AC Barrie, with 1% less protein. The shortest of all CWRS cultivars, AC Superb kernels are large, with similar test weight to Katepwa (AAFRD 2002). This spring (2003), limited seed supplies of AC Superb were available, indicating the demand for this cultivar. The registration and release of AC Superb may be an indication western Canadian wheat breeders are overcoming the challenges associated with *Rht* genes.

This thesis study confirms that losses from lodging can be substantial and CWRS cultivars are susceptible to lodging. Selecting for short plants in early generations, and artificially inducing lodging at the early milk stage will aid in selection to increase genetic lodging resistance. Moreover, data collected for this thesis will be of use for further breeding strategies, and further research, including yield component analysis and genetic studies.

"There. I did it!"

5.1 Literature cited

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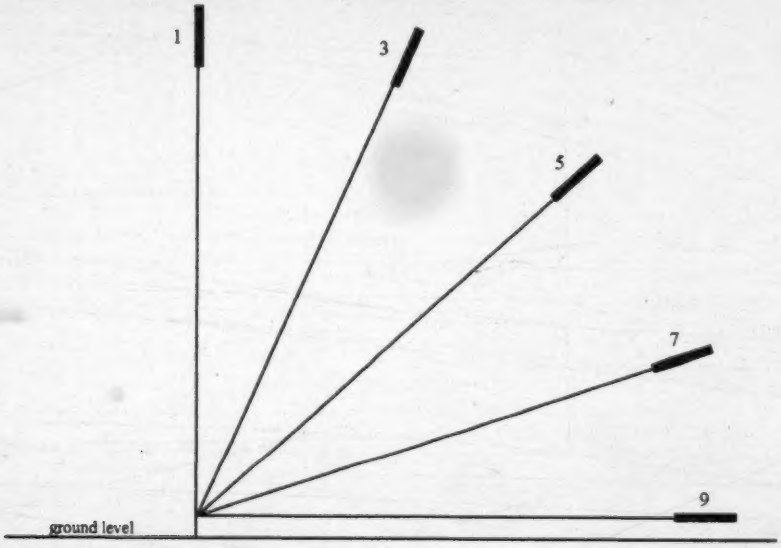
6.0 Appendices

Appendix 6.1. Soil test results for 2001 and 2002 season at the Edmonton Research Station, Edmonton, AB.

	Soil Nutrient Analysis[z] (kg/ha)					
Year	N	P	K	S	pH	EC (dS/m)
2001	75	80	746	38	6.2	0.55
2002	50	20	408	20	6.6	0.47

[z]Analysis provided by Norwest Labs, Edmonton, AB.
Soils were not analyzed in 2000.

Appendix 6.2 Apparatus to artificially induce lodging in a field plot.



Appendix 6.3. Lodging scores assigned according to the position of the crop from ground level, with a score of 1 = vertical stature.

Appendix 6.4. Summation of rank scores over 4 blocks at each treatment (either seeding rate or artificially induced lodging) at Edmonton, AB (2000-2001).

	2000				2001			
	Seeding rate (seeds m-2)		Artificial lodging		Seeding rate (seeds m-2)		Artificial lodging	
Genotype[z]	250	500	GS73-E	GS73-G	250	500	GS73-E	GS73-G
4837.04	45.5	30.5	16.5	11.0	35.5	26.5	6.5	11.0
Kohika	45.5	40.5	21.5	13.5	26.5	26.5	10.0	16.5
C9800L-048	45.5	49.0	16.5	11.0	34.0	35.0	14.0	12.5
Oslo	45.5	38.5	22.5	19.0	26.5	26.5	16.0	12.0
Otane	45.5	45.5	43.0	45.5	26.5	26.5	15.5	13.5
Sapphire	45.5	30.5	16.5	49.5	26.5	26.5	31.0	51.5
AC Foremost	45.5	30.5	39.0	30.0	34.0	35.0	28.0	55.5
N93-0119	45.5	48.0	31.5	37.0	26.5	26.5	41.5	58.0
C9800L-015	45.5	38.5	30.5	21.0	34.0	26.5	42.5	28.5
9207-DB3*D	45.5	42.0	35.5	31.0	34.0	26.5	43.5	43.5
AC 2000	45.5	30.5	39.5	48.0	35.5	44.5	40.0	44.0
9207-DB3*E2	45.5	30.5	44.0	29.0	35.5	54.5	40.0	39.5
ND695	45.5	42.0	28.5	21.5	57.5	46.0	60.5	60.0
AC Domain	45.5	30.5	44.0	60.0	67.5	53.0	61.5	74.0
AC Intrepid	59.0	84.0	66.0	68.0	67.5	73.5	59.0	46.5
AC Vista	57.5	78.0	62.0	45.5	66.0	89.0	71.0	69.0
Laser	45.5	82.5	72.5	75.0	74.5	78.0	65.0	43.5
McKenzie	81.5	76.0	69.0	81.5	90.0	94.0	82.0	86.0
9007-FB01C	59.0	82.0	87.5	71.0	43.0	50.0	64.5	46.5
AC Barrie	56.5	55.5	79.0	65.0	79.0	82.0	80.5	79.5
9107-BT04B	45.5	38.5	75.0	77.5	94.0	84.0	92.0	86.0
AC Splendor	69.5	82.5	72.0	77.5	84.5	84.0	92.0	55.5
9007-FH01C2	45.5	30.5	84.3	67.5	44.5	57.5	80.0	85.5
9007-FH01C4	57.5	52.0	91.0	90.0	69.5	58.5	76.0	91.0
9007-FH01D3	45.5	90.0	84.0	75.0	62.5	69.5	87.5	91.0

From Friedman's multiple comparison test, two genotypes are significantly different if the difference between their rank sums differ by > 64.3, using an experiment-wise error rate of 0.15.
[z]Genotypes listed from lodging tolerant to susceptible, based on GS73-E 2-yr mean.

Appendix 6.5. Mean lodging scores of genotypes immediately following artificial lodging application (initial) and prior to harvest (final); Supplementary to Table 2.5.

	2000				2001			
	GS73-E		GS73-G		GS73-E		GS73-G	
Genotype[z]	Initial	Final	Initial	Final	Initial	Final	Initial	Final
C9800L-048	2 *	1	3 *	1	4	3	5	3
Sapphire	2 *	1	7	6	9 *	5	8	7
C9800L-015	3	2	3	2	8 *	6	7	5
AC Foremost	4 *	3	4	3	7	5	7	7
N93-0119	4	2	5	4	7	6	8	7
ND695	4 *	2	4	2	9	8	9	8
AC Intrepid	5	6	6	8	6	7	5	6
AC Vista	5	6	5	5	8	8	8	8
9007-FB01C	7	8	9	8	9 *	8	9 *	7
9107-BT04B	6	7	7	9	9	9	9	9
9007-FH01C2	7	8	8	8	9	9	9	9
9007-FH01C4	8	9	8	9	9	8	9	9
9007-FH01D3	7	8	8	9	9 *	9	9	9

[z]Genotypes listed from lodging tolerant to susceptible.

*Significant difference ($P < 0.05$) between time of scoring, determined by Wilcoxon analysis by year, lodging treatment and genotype. A blank cell indicates initial and final lodging scores were not different ($P \geq 0.05$).

Appendix 6.6. Culm diameter of the second internode (measured by an environmental scanning electron microscope at 25x magnification) of 13 wheat genotypes grown in Edmonton, AB (2000-2001).

Genotype	Culm diameter (mm)
Kohika	3.15
C9800L-048	3.11
Oslo	3.02
Sapphire	3.73
AC Foremost	3.32
ND695	3.11
AC Domain	2.90
AC Intrepid	3.12
AC Vista	3.13
Laser	3.21
McKenzie	3.13
AC Barrie	3.12
AC Splendor	2.93
F-test	
Var	*
Var*year	ns
SE_{diff}	0.154

Appendix 6.7. Percent sum of squares and degrees of freedom from split plot analysis of eleven agronomic traits evaluated for a lodging experiment over 3 years (2000-2002) at Edmonton, AB.

		Analysis of variance in 2000 (percent of total sum of squares)[z]												
Effects	df	Lodging	Heading	Maturity	Plant height	Septoria	Powdery mildew	Spikes m^{-2}	Kernels spike^{-1}	df	Kernel weight	Test weight	Grain protein	Grain yield
Genotype (G)	24	33***	85***	72***	86***	42***	48***	-	-	24	58***	36***	97***	38***
Block (B)	3	1*	2	2	1	5	0	-	-	2	3	0	0	1
Error A	72	7***	6	10	5	33	26	-	-	48	10	15	2	6*
Treatment (T)	3	29***	0***	4***	0***	2***	2***	-	-	3	12***	16***	0***	31***
G*T	72	19***	1	6***	0*	4	10***	-	-	72	8*	13**	1**	13**
Error B	225	10	2	6	7	13	14	-	-	150	9	20	0	11
CV (%)		38.4	0.9	1.3	1.5	15.3	30.4	-	-		4.9	3.6	1.6	12.7
Total SS		3328.6	3041.1	7246.6	65255.6	551.6	779.5	-	-		5036.0	4600.0	273.6	540323.2

		Analysis of variance in 2001 (percent of total sum of squares)[z]												
Effects	df	Lodging	Heading	Maturity	Plant height	Septoria	Powdery mildew	Spikes m^{-2}	Kernels spike^{-1}	Kernel weight	Test weight	Harvest index	Grain protein	Grain yield
Genotype (G)	24	23***	84***	74***	84***	31***	33***	30***	83***	37***	44***	59***	90***	38***
Block (B)	3	1	2	2	2	8	1	6	0	1	0	0	1	2
Error A	72	3	11	17	6	34	29	9	5	7	5	4	4	6
Treatment (T)	3	60***	0**	1***	1***	1*	1**	15***	2***	34***	37***	20***	0**	40***
G*T	72	9***	1	2**	1	6	20***	11	3*	9***	8***	6***	2*	6***
Error B	225	4	2	4	1	20	16	29	7	12	6	10	3	8
CV (%)		17.6	0.7	1.2	1.7	26.9	17.6	16.6	6.9	6.1	1.4	7.5	2.8	11.7
Total SS		3429.7	2295.7	9658.9	39034.5	794.2	46.3	5003127.1	20648.4	9574.4	4290.3	1.97	333.0	596213.5

Appendix 6.7. Continued...

		Analysis of variance in 2002 (percent of total sum of squares)[z]												
Effects	df	Lodging	Heading	Maturity	Plant height	Septoria	Powdery mildew	Spikes m^{-2}	Kernels $spike^{-1}$	Kernel weight	Test weight	Harvest index	Grain protein	Grain yield
Genotype (G)	24	.	81***	88***	49***	.	.	11***	37***	84***	79***	41***	76***	34***
Block (B)	3	.	0	1	9	.	.	0	12	1	2	11	13	23
Error A	72	.	9	5	23	.	.	5	9	3	7	9	6	28
Treatment (T)	3	.	3***	2***	9***	.	.	58***	28***	5***	0**	14**	1	2***
G*T	72	.	2	1	2**	.	.	10***	5**	2	5***	8*	0	3
Error B	225	.	5	3	5	.	.	16	9	5	6	17	3	10
CV (%)		.	1.2	1.1	3.3	.	.	18.2	10.5	3.6	0.5	5.7	1.6	10.8
Total SS		.	2046.0	9428.9	16054.0	.	.	7201801.5	19072.5	8574.0	477.8	1.04	177.4	109039.0

[z]A value of zero results from rounding 0.01 to 0.49 downward to zero.
*, **, ***: effects significant at $P < 0.05$, 0.01, or 0.001, respectively.

Appendix 6.8. Percent sum of squares (SS) and degrees of freedom of combined-year analysis for agronomic traits presented in *Table 2.7* that were evaluated under artificially induced lodging at GS73-E in Edmonton, AB (2000-2001).

		Combined-year analysis of variance (percent of total sum of squares)			
Effects	df	Plant height[z]	Kernel weight	Test weight	Grain yield
Year	1	26***	4	1	17**
Block (year)	6	1	6	2	2
Genotype	24	65***	60***	41***	62***
Genotype*year	24	3**	11	18	6
Error	144	5	19	38	13
CV (%)		3.6	1.0	3.5	4.0
Total SS		36453.5	2880.8	2248.0	255372.4

[z]Evaluated under the recommended seeding rate and no artificially induced lodging.
, *: effects or significant at $P < 0.01$, or 0.001, respectively.
Error = genotype*block(year)

Appendix 6.9. Percent sum of squares (SS) and degrees of freedom of combined-year analysis for culm traits measured visually or with a calliper (*Tables 3.2 & 3.3*) of 13 spring wheat genotypes grown in Edmonton, AB (2000-2001).

			Combined-year analysis of variance (percent of total sum of squares)[z]							
		Final	Plant	No. of	Internode length			Internode diameter		
Effects	df	lodging	height	internodes	2nd	3rd	4th	1st	2nd	4th
Year	1	12***	20**	9	5*	8	2*	5	10	7*
Block(year)	4	2	0	2	2	1	1	1	1	0
Genotype	12	62***	64***	17**	31***	35***	20***	17***	15*	12*
Genotype*year	12	6*	3*	6	4	5	4	4	10	5
[z]Experimental error	24	-	3	8	5	5	7	11	12	4
[y]Sampling error	312	-	7	47	40	39	55	51	42	57
Residual error	24	18	3	11	3	7	11	11	10	15
CV (%)		28.7	4.6	8.5	25.8	26.6	39.1	16.6	10.9	33.6
Total SS		906.1	79952.1	123.7	2881.5	8871.8	24102.01	10.3	8.7	58.1

*, **, ***: effects significant at $P < 0.05$, 0.01, or 0.001, respectively.
[z]experimental error = year*block*genotype;
[y]sampling error = sample number(year*block*genotype).

Appendix 6.10. Percent sum of squares (SS) and degrees of freedom of combined-year analysis for culm traits measured with an environmental scanning electron microscope (*Table 3.4*) of 13 spring wheat genotypes grown in Edmonton, AB (2000-2001).

		Combined-year analysis of variance (percent of total sum of squares)[z]					
		2nd internode	No. of vascular bundles		Culm wall	Lumen	Sclerenchyma
Effects	df	Culm diameter	Parenchyma	Total	thickness	diameter	ring thickness
Year	1	12*	19	23	18	1	21
Block(year)	2	0	2	7	0	1	1
Genotype	12	31*	29*	17*	18*	27	15
Genotype*year	12	15	10	16	4	19	10
[y]Experimental error	12	9	10	6	6	11	9
[y]Sampling error	156	25	25	27	48	34	37
Residual error	12	8	5	4	6	7	7
CV (%)		6.4	7.3	7.4	16.6	14.8	13.4
Total SS		25902.9	2694.1	4768.4	4379.6	31598.1	38812.8

[z]A value of zero results from rounding 0.01 to 0.49 downward to zero.
*: effects significant at $P < 0.05$.
[z]Experimental error = year*block*genotype;
sampling error = sample number(year*block*genotype).

Appendix 6.11. Percent sum of squares (SS) and degrees of freedom for culm traits analyzed by year in Chapter 3 of 13 spring wheat genotypes grown in Edmonton, AB (2000-2001).

		Analysis of variance (percent of total sum of squares)[z]							
								Vascular bundles in	
		Adventitious	1st internode length		3rd internode diameter			sclerenchyma ring	
Effect	df	roots	2000	2001	2000	2001	df	2000	2001
Block	2	5	1	1	3	0	1	5	8
Genotype	12	12	20**	9*	40**	26**	12	39*	30**
[z]Experimental error	24	14	11	8	18	15	12	11	4
[z]Sampling error	156	69	68	82	38	59	78	45	58
CV(%)		92.9	52.6	55.3	11.7	10		21.9	23.7
Total SS		622.4	922.3	337.1	5.4	3.3		810.9	997.4

[z]Experimental error = block*genotype ; sampling error = sample number(block*genotype).
*, **: effects significant at $P < 0.05$, or 0.01, respectively.

Appendix 6.12. Combined-year model used for Chapter 4.

Effect		df
Year	(Y-1)	2
Rep[Y]	(R-1)Y	9
Treatment	(T-1)	1
Y*T (Error A)	(Y-1)(T-1)	2
T*Rep[Y]	(T-1)(R-1)Y	9
Genotype	(G-1)	24
Y*G (Error B)	(Y-1)(G-1)	48
T*G	(T-1)(G-1)	24
Y*T*G (Error C)	(Y-1)(T-1)(G-1)	48
G*Rep[Y*T]	(G-1)(R-1)YT	432

Appendix 6.13. Least-square means of agronomic traits measured on 25 spring wheat genotypes under 4 treatments to evaluate lodging susceptibility at Edmonton, AB (2000).

Genotype[z]	Treatment	Final lodging (1 to 9)	Heading (days)	Maturity (days)	Plant height (cm)	Septoria (1 to 9)	Kernel weight (mg)	Test weight (kg hL^{-1})	Grain protein (%)	Grain yield (t ha^{-1})
4837.04	Control	1	65	122	87	2	41	76	12.8	6.26
	Seedx2	1	65	120	88	3	37	76	-	6.69
	GS73-E	1	65	122	-	3	40	76	12.6	5.72
	GS73-G	1	65	121	-	3	39	75	-	5.68
Kohika	Control	1	62	114	78	5	37	75	12.2	6.09
	Seedx2	1	61	113	77	5	38	75	-	5.65
	GS73-E	1	62	114	-	5	39	75	12.4	5.70
	GS73-G	1	62	114	-	5	37	75	-	5.40
C9800L-048	Control	1	58	114	77	4	34	74	11.9	6.07
	Seedx2	2	58	115	79	5	33	74	-	5.06
	GS73-E	1	59	114	-	5	36	74	11.8	5.97
	GS73-G	1	59	114	-	5	34	74	-	5.96
Oslo	Control	1	59	113	88	4	34	74	12.6	5.70
	Seedx2	1	58	113	90	4	34	74	-	5.42
	GS73-E	2	59	114	-	4	33	73	12.8	5.20
	GS73-G	2	59	114	-	4	33	74	-	4.96
Otane	Control	1	65	118	87	5	38	74	11.8	5.61
	Seedx2	2	64	118	87	5	35	73	-	4.72
	GS73-E	3	65	119	-	5	36	72	12.4	4.23
	GS73-G	5	65	120	-	5	32	68	-	2.82
Sapphire	Control	1	68	125	90	3	39	75	11.7	6.31
	Seedx2	1	68	124	88	4	38	75	-	6.57
	GS73-E	1	68	124	-	3	39	75	11.9	5.90
	GS73-G	6	68	125	-	3	32	68	-	3.38
C9800L-015	Control	1	62	116	84	3	34	77	12.0	6.64
	Seedx2	1	63	116	83	3	33	77	-	6.66
	GS73-E	2	63	116	-	3	35	76	12.3	6.15
	GS73-G	2	63	116	-	3	35	77	-	6.23
AC Foremost	Control	1	63	119	89	4	41	76	11.9	5.98
	Seedx2	1	62	118	88	4	37	75	-	6.45
	GS73-E	3	62	120	-	4	38	74	12.1	5.07
	GS73-G	3	62	121	-	4	39	74	-	5.11
N93-119	Control	1	60	121	85	2	36	77	13.7	6.35
	Seedx2	2	59	122	85	2	35	76	-	6.22
	GS73-E	2	60	123	-	3	35	76	14.4	5.25
	GS73-G	4	60	123	-	3	34	74	-	4.30
9207-DB3*E2	Control	1	62	118	96	5	37	75	14.5	5.08
	Seedx2	1	62	116	95	6	35	74	-	5.75
	GS73-E	3	62	118	-	6	31	71	14.8	3.38
	GS73-G	3	63	119	-	6	35	71	-	4.06
9207-DB3*D	Control	1	64	117	99	3	40	78	14.6	5.21
	Seedx2	2	64	118	96	4	39	77	-	5.10
	GS73-E	3	64	118	-	4	38	76	14.8	3.97
	GS73-G	3	64	119	-	4	38	75	-	3.94
AC 2000	Control	1	67	120	97	4	41	76	12.1	6.31
	Seedx2	1	66	118	98	4	40	76	-	6.25
	GS73-E	3	67	125	-	4	40	72	12.7	4.71
	GS73-G	6	67	126	-	5	35	70	-	3.30
ND695	Control	1	62	125	94	2	39	78	13.9	5.46
	Seedx2	2	61	125	94	2	38	77	-	5.85
	GS73-E	2	62	125	-	3	38	76	14.1	5.27
	GS73-G	2	62	125	-	2	38	77	-	5.45

Appendix 6.13. Continued...

Genotype[z]	Treatment	Final lodging (1 to 9)	Heading (days)	Maturity (days)	Plant height (cm)	Septoria (1 to 9)	Kernel weight (mg)	Test weight (kg hL^{-1})	Grain protein (%)	Grain yield (t ha^{-1})
AC Domain	Control	1	60	114	99	4	35	74	14.7	4.77
	Seedx2	1	59	114	97	4	32	74	-	5.23
	GS73-E	4	60	115	-	4	32	72	14.9	3.86
	GS73-G	7	60	115	-	4	29	70	-	2.84
AC Intrepid	Control	2	59	114	115	3	38	75	14.2	5.01
	Seedx2	5	60	112	114	4	35	71	-	3.78
	GS73-E	6	59	115	-	3	35	72	14.6	3.69
	GS73-G	8	60	114	-	4	35	72	-	3.71
AC Vista	Control	1	62	116	98	3	44	75	11.9	5.88
	Seedx2	5	62	117	97	4	39	74	-	5.01
	GS73-E	6	62	117	-	3	39	73	12.2	4.77
	GS73-G	5	63	116	-	3	42	74	-	4.82
Laser	Control	1	58	110	109	4	35	74	14.0	6.24
	Seedx2	5	58	110	106	4	33	70	-	4.13
	GS73-E	7	58	111	-	4	31	69	14.4	3.78
	GS73-G	8	59	112	-	4	28	62	-	2.12
9007-FB01C	Control	3	66	116	107	4	30	74	15.2	3.70
	Seedx2	5	65	119	107	4	29	73	-	3.46
	GS73-E	8	65	119	-	4	29	72	15.8	2.58
	GS73-G	8	65	119	-	5	26	69	-	2.28
McKenzie	Control	3	59	112	108	4	32	74	14.1	4.71
	Seedx2	5	58	113	105	4	29	68	-	3.63
	GS73-E	7	59	114	-	4	29	69	15.1	3.06
	GS73-G	9	59	114	-	3	27	65	-	2.40
AC Barrie	Control	2	61	116	111	4	35	73	15.2	4.14
	Seedx2	3	61	114	108	4	34	74	-	3.70
	GS73-E	8	61	116	-	5	33	65	15.3	2.67
	GS73-G	8	61	116	-	4	35	65	-	2.87
9107-BT04B	Control	1	62	115	115	4	42	73	15.8	3.79
	Seedx2	1	61	114	113	4	42	73	-	4.19
	GS73-E	7	62	115	-	4	37	66	16.4	2.63
	GS73-G	8	62	115	-	4	36	65	-	2.29
AC Splendor	Control	2	59	112	113	3	36	73	15.4	4.46
	Seedx2	6	58	111	110	3	33	69	-	4.69
	GS73-E	7	59	113	-	4	32	69	15.1	3.48
	GS73-G	9	59	113	-	4	30	68	-	3.18
9007-FH01C2	Control	1	61	116	118	3	38	77	15.9	4.72
	Seedx2	1	62	117	114	4	37	76	-	4.90
	GS73-E	8	62	123	-	4	34	73	16.2	2.99
	GS73-G	8	62	123	-	4	35	75	-	4.72
9007-FH01C4	Control	1	60	115	115	4	36	76	15.2	4.98
	Seedx2	3	61	116	118	5	34	75	-	4.39
	GS73-E	9	61	122	-	4	31	73	15.5	2.64
	GS73-G	9	60	120	-	5	26	68	-	2.17
9007-FH01D3	Control	1	64	115	123	3	36	76	16.2	4.49
	Seedx2	6	63	116	122	4	33	75	-	3.72
	GS73-E	8	63	120	-	4	30	72	15.9	2.77
	GS73-G	9	62	119	-	4	31	72	-	3.34
SE(treatment)[y]		**0.2**	**0.1**	**0.2**	**0.2**	**0.1**	**0.3**	**0.4**	**0.05**	**0.10**
SE(genotype)[y]		**0.7**	**0.4**	**1.0**	**1.0**	**0.4**	**1.1**	**1.6**	**0.21**	**0.36**

[z]Genotypes listed in increasing lodging susceptibility.

[y]Standard error of the difference between two least-square means.

Appendix 6.14. Least-square means of agronomic traits measured on 25 spring wheat genotypes under 4 treatments to evaluate lodging susceptibility at Edmonton, AB (2001).

Genotype[z]	Treatment	Final lodging (1 to 9)	Heading (days)	Maturity (days)	Plant height (cm)	Septoria (1 to 9)	Spike m^{-2}	Kernels $spike^{-1}$	Kernel weight (mg)	Test weight ($kg\ hL^{-1}$)	Grain protein (%)	Harvest index	Grain yield ($t\ ha^{-1}$)
4837.04	Control	1	64	117	77	3	459	40	40	76	13.6	0.44	4.69
	Seedx2	1	64	117	80	3	457	40	38	76	-	0.44	5.43
	GS73-E	2	64	117	-	3	452	43	38	76	12.9	0.43	4.68
	GS73-G	2	64	118	-	3	509	41	38	75	-	0.42	4.92
Kohika	Control	1	60	111	68	6	415	47	39	77	12.0	0.51	4.83
	Seedx2	1	60	111	70	6	617	47	37	77	-	0.50	6.28
	GS73-E	2	60	112	-	6	373	45	37	76	12.5	0.50	4.57
	GS73-G	3	61	113	-	5	575	44	37	76	-	0.45	4.93
C9800L-048	Control	1	59	110	75	4	433	44	38	78	11.5	0.51	5.33
	Seedx2	1	59	108	76	5	563	43	36	77	-	0.50	5.78
	GS73-E	3	59	109	-	4	464	40	36	76	11.5	0.45	4.37
	GS73-G	3	59	109	-	5	493	42	34	75	-	0.47	5.00
Oslo	Control	1	58	110	76	3	429	42	38	78	12.3	0.50	4.97
	Seedx2	1	57	109	78	3	576	43	35	78	-	0.49	5.87
	GS73-E	3	58	110	-	3	401	41	37	76	12.6	0.46	4.37
	GS73-G	3	58	111	-	4	478	41	36	77	-	0.46	5.29
Otane	Control	1	64	122	72	5	339	48	42	77	12.1	0.52	4.74
	Seedx2	1	64	121	73	5	377	42	42	77	-	0.51	5.40
	GS73-E	3	64	121	-	5	341	45	38	75	12.6	0.50	3.92
	GS73-G	3	64	121	-	5	426	44	38	75	-	0.45	4.48
Sapphire	Control	1	66	124	79	3	326	58	41	69	12.6	0.46	5.40
	Seedx2	1	66	124	81	3	402	54	39	69	-	0.47	6.63
	GS73-E	5	66	122	-	3	290	48	35	65	12.5	0.37	3.35
	GS73-G	7	66	122	-	3	348	49	30	63	-	0.34	3.22
C9800L-015	Control	1	61	111	74	3	471	39	38	78	13.3	0.46	5.39
	Seedx2	1	61	111	79	3	516	37	38	79	-	0.44	5.91
	GS73-E	6	61	113	-	3	548	37	32	75	13.0	0.41	4.01
	GS73-G	5	60	112	-	3	485	33	33	75	-	0.40	4.52
AC Foremost	Control	1	62	119	73	3	387	44	43	78	12.3	0.48	4.89
	Seedx2	1	62	120	75	4	443	45	44	77	-	0.48	5.96
	GS73-E	5	62	120	-	3	384	44	37	74	12.7	0.42	3.60
	GS73-G	7	62	119	-	3	430	43	35	73	-	0.42	4.14
N93-119	Control	1	61	120	76	1	604	39	36	77	14.3	0.45	5.14
	Seedx2	1	61	120	75	2	695	36	38	78	-	0.47	5.71
	GS73-E	6	61	120	-	2	483	32	33	74	14.4	0.39	3.93
	GS73-G	7	61	120	-	2	647	33	34	73	-	0.40	3.92
9207-DB3*E2	Control	1	61	113	84	3	443	37	40	78	14.2	0.44	4.18
	Seedx2	2	61	113	87	4	578	37	40	79	-	0.46	4.66
	GS73-E	6	61	111	-	3	392	35	29	72	14.7	0.38	2.56
	GS73-G	6	61	110	-	4	492	36	31	71	-	0.37	2.82
9207-DB3*D	Control	1	62	116	82	3	450	32	41	79	13.8	0.42	3.69
	Seedx2	1	62	116	84	2	484	31	42	79	-	0.42	4.87
	GS73-E	6	62	114	-	3	375	28	34	75	14.4	0.32	2.65
	GS73-G	7	62	114	-	3	503	29	36	76	-	0.34	3.34
AC 2000	Control	1	65	119	83	4	397	40	46	76	13.0	0.44	5.14
	Seedx2	2	65	119	87	3	436	46	40	75	-	0.42	5.48
	GS73-E	6	65	118	-	4	378	40	35	71	13.1	0.32	3.60
	GS73-G	7	65	119	-	4	424	43	33	69	-	0.34	3.16
ND695	Control	2	60	119	85	2	575	32	39	78	13.9	0.42	5.43
	Seedx2	2	59	120	84	2	693	35	37	79	-	0.44	5.74
	GS73-E	8	60	119	-	2	520	31	31	74	14.2	0.36	3.60
	GS73-G	8	60	119	-	3	589	31	31	75	-	0.36	3.82

Appendix 6.14. Continued...

Genotype[z]	Treatment	Final lodging (1 to 9)	Heading (days)	Maturity (days)	Plant height (cm)	Septoria (1 to 9)	Spike m^{-2}	Kernels $spike^{-1}$	Kernel weight (mg)	Test weight ($kg\ hL^{-1}$)	Grain protein (%)	Harvest index	Grain yield ($t\ ha^{-1}$)
AC Domain	Control	3	60	110	96	3	547	27	37	78	15.0	0.40	3.78
	Seedx2	2	60	110	92	2	577	28	37	78	-	0.40	4.32
	GS73-E	8	60	110	-	2	523	27	32	74	14.7	0.33	2.31
	GS73-G	8	59	109	-	3	588	25	29	73	-	0.34	2.80
AC Intrepid	Control	3	59	110	93	3	489	31	40	77	14.9	0.42	4.25
	Seedx2	3	59	112	96	3	538	28	41	78	-	0.43	4.63
	GS73-E	7	59	110	-	2	350	28	37	74	15.0	0.34	2.94
	GS73-G	6	59	111	-	3	485	28	38	75	-	0.37	3.55
AC Vista	Control	3	62	120	84	3	365	41	45	75	13.0	0.45	5.48
	Seedx2	4	62	120	86	3	500	39	46	76	-	0.46	5.55
	GS73-E	8	62	116	-	3	388	38	36	70	12.9	0.40	3.22
	GS73-G	8	62	115	-	3	437	39	38	70	-	0.42	3.46
Laser	Control	3	58	110	94	3	433	37	42	77	14.0	0.45	5.18
	Seedx2	3	57	109	96	4	417	39	43	77	-	0.46	5.59
	GS73-E	8	58	109	-	4	389	35	35	71	14.4	0.37	3.06
	GS73-G	7	58	109	-	4	472	34	39	74	-	0.37	4.16
9007-FB01C	Control	2	65	117	88	3	507	31	32	77	15.2	0.31	3.55
	Seedx2	2	65	117	91	3	629	30	31	77	-	0.33	3.99
	GS73-E	8	65	115	-	3	522	28	27	72	14.7	0.27	2.66
	GS73-G	7	65	116	-	3	539	29	26	73	-	0.26	2.65
McKenzie	Control	4	60	111	97	3	603	33	33	77	14.6	0.40	4.39
	Seedx2	4	60	111	100	3	616	33	33	77	-	0.41	4.46
	GS73-E	9	60	109	-	3	437	32	25	70	14.2	0.27	2.19
	GS73-G	9	60	109	-	5	434	32	24	69	-	0.26	2.14
AC Barrie	Control	3	62	113	95	3	459	33	38	78	14.1	0.38	3.87
	Seedx2	3	62	112	96	4	586	33	37	78	-	0.40	4.67
	GS73-E	9	62	113	-	3	459	29	30	73	14.7	0.28	2.25
	GS73-G	9	62	113	-	3	566	28	31	75	-	0.32	2.51
9107-BT04B	Control	4	61	111	98	4	423	28	40	77	16.1	0.40	3.95
	Seedx2	3	61	110	99	4	604	28	40	77	-	0.40	4.18
	GS73-E	9	62	109	-	4	505	27	31	71	15.8	0.31	2.35
	GS73-G	9	61	109	-	5	436	27	31	71	-	0.27	2.60
AC Splendor	Control	3	59	109	96	3	418	30	39	76	15.2	0.40	3.58
	Seedx2	3	58	108	99	4	554	29	38	77	-	0.40	4.22
	GS73-E	9	59	109	-	3	389	27	33	72	14.8	0.34	2.29
	GS73-G	7	58	109	-	3	508	28	33	73	-	0.36	2.98
9007-FH01C2	Control	2	62	116	97	2	365	33	39	78	15.9	0.35	3.36
	Seedx2	2	62	115	101	3	514	33	38	78	-	0.34	4.19
	GS73-E	9	62	114	-	3	388	32	31	74	15.6	0.29	2.04
	GS73-G	9	62	115	-	2	504	30	31	75	-	0.32	2.62
9007-FH01C4	Control	2	60	114	94	2	441	32	37	78	15.4	0.38	3.78
	Seedx2	2	60	112	98	2	583	33	36	79	-	0.38	4.70
	GS73-E	8	60	110	-	3	450	33	31	74	15.2	0.32	2.56
	GS73-G	9	60	110	-	3	491	32	31	74	-	0.33	2.62
9007-FH01D3	Control	3	62	114	96	2	460	33	36	78	15.7	0.36	3.33
	Seedx2	2	62	115	100	2	548	33	36	78	-	0.36	4.13
	GS73-E	9	62	112	-	3	450	32	32	75	15.3	0.31	1.94
	GS73-G	9	62	114	-	4	587	31	31	74	-	0.31	2.22
SE(treatment)[y]		**0.1**	**0.1**	**0.2**	**0.1**	**0.1**	**14.7**	**0.3**	**0.3**	**0.1**	**0.06**	**0.004**	**0.06**
SE(genotype)[y]		**0.5**	**0.3**	**0.9**	**1.0**	**0.6**	**29.5**	**1.4**	**1.2**	**0.6**	**0.23**	**0.021**	**0.26**

[z]Genotypes listed in increasing lodging susceptibility.

[y]Standard error of the difference between two least-square means.

Appendix 6.15. Least-square means of agronomic traits measured on 25 spring wheat genotypes under 4 treatments to evaluate lodging susceptibility at Edmonton, AB (**2002**).

Genotype[z]	Treatment	Final lodging (1 to 9)	Heading (days)	Maturity (days)	Plant height (cm)	Spike m^{-2}	Kernels $spike^{-1}$	Kernel weight (mg)	Test weight (kg hL^{-1})	Grain protein (%)	Harvest index	Grain yield (t ha^{-1})
4837.04	Control	1	58	105	54	336	28	41	80	15.1	0.52	2.38
	Seedx2	1	57	102	51	678	21	39	80	-	0.50	2.21
	GS73-E	1	58	106	-	341	28	41	80	15.3	0.52	2.33
	GS73-G	1	57	105	-	314	29	42	80	-	0.54	2.18
Kohika	Control	1	58	105	52	291	28	43	81	14.5	0.55	2.22
	Seedx2	1	56	105	49	475	20	41	81	-	0.52	2.18
	GS73-E	1	57	105	-	284	27	43	81	14.8	0.54	2.20
	GS73-G	1	57	105	-	307	29	43	81	-	0.53	2.10
C9800L-048	Control	1	54	97	53	365	26	36	80	14.5	0.50	1.88
	Seedx2	1	53	97	47	665	18	34	80	-	0.40	1.63
	GS73-E	1	54	97	-	386	27	36	80	14.5	0.47	1.94
	GS73-G	1	54	97	-	365	25	37	80	-	0.49	1.90
Oslo	Control	1	53	97	50	308	26	38	78	14.0	0.53	2.09
	Seedx2	1	52	96	50	605	17	35	79	-	0.48	1.71
	GS73-E	1	53	97	-	350	30	37	78	14.0	0.52	1.95
	GS73-G	1	54	98	-	354	29	38	78	-	0.54	1.95
Otane	Control	1	58	104	56	254	33	44	80	14.5	0.57	2.19
	Seedx2	1	57	103	49	468	23	43	81	-	0.51	2.10
	GS73-E	1	58	104	-	260	34	44	81	14.0	0.56	2.45
	GS73-G	1	58	105	-	247	33	45	80	-	0.56	2.27
Sapphire	Control	1	61	114	57	242	47	47	78	13.5	0.57	2.80
	Seedx2	1	61	112	56	399	36	45	80	-	0.54	3.17
	GS73-E	1	62	114	-	264	46	46	78	13.5	0.55	2.91
	GS73-G	1	61	114	-	279	45	46	78	-	0.55	2.74
C9800L-015	Control	1	56	98	48	367	30	35	81	14.8	0.54	2.18
	Seedx2	1	55	98	45	559	20	34	81	-	0.47	1.99
	GS73-E	1	56	98	-	321	27	36	81	14.8	0.52	2.00
	GS73-G	1	56	98	-	352	33	34	81	-	0.50	2.31
AC Foremost	Control	1	55	108	51	307	29	43	79	14.8	0.54	1.96
	Seedx2	1	54	107	48	462	19	39	79	-	0.49	1.80
	GS73-E	1	55	108	-	290	29	42	79	14.9	0.53	1.82
	GS73-G	1	55	108	-	295	28	43	79	-	0.54	2.02
N93-119	Control	1	56	108	57	387	31	39	81	15.5	0.55	2.30
	Seedx2	1	55	107	55	420	26	39	81	-	0.53	2.11
	GS73-E	1	57	108	-	338	31	40	81	15.7	0.54	2.34
	GS73-G	1	56	108	-	371	29	39	81	-	0.51	2.21
9207-DB3*E2	Control	1	56	102	58	384	26	39	80	15.3	0.52	2.25
	Seedx2	1	55	100	52	667	19	38	80	-	0.44	1.85
	GS73-E	1	56	103	-	336	27	40	80	15.4	0.51	2.07
	GS73-G	1	56	102	-	346	24	39	80	-	0.52	1.90
9207-DB3*D	Control	1	56	104	60	317	27	40	82	15.7	0.53	2.14
	Seedx2	1	56	102	54	484	18	38	82	-	0.51	1.73
	GS73-E	1	56	104	-	366	23	39	82	15.8	0.53	1.93
	GS73-G	1	57	104	-	397	22	40	82	-	0.50	1.85
AC 2000	Control	1	58	105	61	313	30	43	80	14.3	0.49	2.21
	Seedx2	1	57	103	55	507	25	40	80	-	0.49	1.80
	GS73-E	1	58	105	-	309	32	44	80	14.3	0.50	2.10
	GS73-G	1	58	105	-	317	33	43	80	-	0.51	2.21
ND695	Control	1	57	110	58	361	33	39	80	15.1	0.57	2.39
	Seedx2	1	57	109	56	451	28	38	80	-	0.55	2.57
	GS73-E	1	58	110	-	395	31	38	80	15.1	0.56	2.55
	GS73-G	1	58	110	-	333	32	40	80	-	0.56	2.60

Appendix 6.15. Continued...

Genotype[z]	Treatment	Final lodging (1 to 9)	Heading (days)	Maturity (days)	Plant height (cm)	Spike m^{-2}	Kernels $spike^{-1}$	Kernel weight (mg)	Test weight ($kg\ hL^{-1}$)	Grain protein (%)	Harvest index	Grain yield ($t\ ha^{-1}$)
AC Domain	Control	1	55	99	63	398	29	34	80	14.9	0.51	2.00
	Seedx2	1	54	98	60	560	22	32	80	-	0.48	1.89
	GS73-E	1	55	100	-	345	28	34	80	15.0	0.51	1.93
	GS73-G	1	55	100	-	424	30	35	80	-	0.51	1.82
AC Intrepid	Control	1	54	96	63	347	33	36	79	14.4	0.52	2.06
	Seedx2	1	54	96	55	621	21	33	79	-	0.48	1.83
	GS73-E	1	54	97	-	329	33	36	79	14.5	0.52	1.88
	GS73-G	1	54	96	-	339	34	37	79	-	0.51	1.94
AC Vista	Control	1	57	103	62	345	32	45	78	13.9	0.55	2.38
	Seedx2	1	57	104	58	547	18	41	79	-	0.52	2.30
	GS73-E	1	58	105	-	329	28	44	79	14.0	0.54	2.19
	GS73-G	1	57	106	-	272	35	45	78	-	0.54	2.34
Laser	Control	1	52	96	59	340	27	37	78	15.7	0.50	1.79
	Seedx2	1	51	96	56	582	15	36	79	-	0.43	1.50
	GS73-E	1	52	97	-	371	26	38	78	15.7	0.51	1.77
	GS73-G	1	51	96	-	352	28	38	78	-	0.50	1.78
9007-FB01C	Control	1	57	105	55	392	27	29	81	16.1	0.46	1.75
	Seedx2	1	56	103	52	536	22	28	80	-	0.49	1.66
	GS73-E	1	58	105	-	387	28	29	80	16.1	0.50	1.85
	GS73-G	1	58	105	-	405	27	29	81	-	0.50	1.76
McKenzie	Control	1	54	100	65	346	26	32	80	15.1	0.49	1.84
	Seedx2	1	52	98	60	655	19	30	80	-	0.45	1.66
	GS73-E	1	53	99	-	399	26	32	80	15.2	0.50	1.71
	GS73-G	1	53	99	-	398	28	33	81	-	0.48	1.77
AC Barrie	Control	1	57	101	64	347	30	35	80	14.6	0.50	1.95
	Seedx2	1	57	98	61	701	19	31	80	-	0.45	1.73
	GS73-E	1	58	102	-	313	27	34	81	14.6	0.50	1.85
	GS73-G	1	57	101	-	375	31	35	80	-	0.49	1.88
9107-BT04B	Control	1	57	99	65	368	24	37	80	15.4	0.49	1.91
	Seedx2	1	57	97	59	826	16	33	79	-	0.42	1.51
	GS73-E	1	58	99	-	417	26	37	81	15.7	0.47	1.90
	GS73-G	1	57	99	-	392	26	38	80	-	0.50	1.96
AC Splendor	Control	1	54	96	62	293	31	32	79	15.2	0.49	1.72
	Seedx2	1	52	96	57	516	25	31	78	-	0.45	1.65
	GS73-E	1	54	97	-	274	30	32	79	15.5	0.50	1.57
	GS73-G	1	54	97	-	243	30	31	78	-	0.50	1.55
9007-FH01C2	Control	1	56	107	63	390	27	37	81	16.7	0.44	1.51
	Seedx2	1	56	105	57	599	20	35	81	-	0.39	1.50
	GS73-E	1	57	106	-	346	25	36	81	16.7	0.46	1.63
	GS73-G	1	57	107	-	310	26	38	80	-	0.46	1.56
9007-FH01C4	Control	1	55	104	62	345	25	35	81	16.5	0.47	1.91
	Seedx2	1	54	103	54	738	16	32	81	-	0.38	1.60
	GS73-E	1	55	104	-	345	27	34	81	16.5	0.48	1.87
	GS73-G	1	55	104	-	343	28	36	81	-	0.48	1.83
9007-FH01D3	Control	1	55	105	61	383	25	35	80	16.5	0.46	1.69
	Seedx2	1	55	102	53	635	15	31	80	-	0.39	1.39
	GS73-E	1	56	105	-	372	24	35	80	16.5	0.46	1.67
	GS73-G	1	56	106	-	370	26	35	80	-	0.48	1.74
SE(treatment)[y]		**0.0**	**0.1**	**0.2**	**0.2**	**9.4**	**0.4**	**0.2**	**0.1**	**0.03**	**0.004**	**0.03**
SE(genotype)[y]		**0.0**	**0.4**	**1.0**	**1.2**	**24.4**	**1.7**	**0.8**	**0.2**	**0.20**	**0.013**	**0.15**

[z]Genotypes listed in increasing lodging susceptibility.

[y]Standard error of the difference between two least-square means.

Appendix 6.16. Least-square means of culm traits measured on 13 spring wheat genotypes under a recommended seeding rate and no artificial lodging at Edmonton, AB (2000).

Genotype[z]	Plant height (cm)	No. of internodes	Internode length (cm)				Internode diameter (mm)				
			1st	2nd	3rd	4th	1st	2nd - calliper	2nd - ESEM	3rd	4th
Kohika	77	4.9	2.2	6.5	10.0	16.3	2.52	3.22	3.03	0.35	0.36
C9800L-048	78	4.6	3.6	7.5	12.2	9.6	2.30	2.91	2.91	0.33	0.20
Oslo	86	4.9	3.8	6.9	10.0	13.3	2.35	3.08	3.19	0.34	0.29
Sapphire	86	4.7	4.6	8.3	13.5	12.6	2.96	3.59	3.52	0.40	0.29
AC Foremost	88	5.1	4.3	7.5	10.7	20.1	2.47	2.98	3.17	0.33	0.37
ND695	92	4.9	3.4	8.6	13.6	19.3	2.42	2.90	2.79	0.33	0.28
AC Domain	105	5.1	2.7	8.5	14.5	23.5	2.02	2.68	2.69	0.28	0.28
AC Intrepid	111	4.7	5.0	11.1	19.4	18.3	2.39	2.93	3.23	0.31	0.21
AC Vista	98	4.7	4.3	8.1	15.7	17.0	2.37	3.25	3.04	0.34	0.26
Laser	112	5.8	2.7	6.4	9.3	15.1	2.22	2.88	3.24	0.34	0.37
McKenzie	104	4.7	5.4	11.0	16.7	16.0	2.40	2.74	2.93	0.28	0.18
AC Barrie	113	4.9	3.2	10.3	16.2	26.6	2.18	2.93	2.93	0.29	0.26
AC Splendor	111	4.7	4.9	10.3	18.5	20.3	2.20	2.79	2.81	0.27	0.22
SE[y]	**3.2**	**0.23**	**0.74**	**0.72**	**2.04**	**4.29**	**0.23**	**0.34**	**0.26**	**0.25**	**0.73**

Appendix 6.16. Continued.....

Genotype[z]	No. of vascular bundles			Culm wall thickness (mm)	Lumen diameter (mm)	Sclerenchyma ring thickness (μm)
	Sclerenchyma	Parenchyma	Total			
Kohika	12	28	40	0.67	1.68	72.4
C9800L-048	9	26	35	0.67	1.58	64.9
Oslo	8	29	37	0.74	1.71	69.9
Sapphire	6	29	35	0.78	1.97	66.5
AC Foremost	10	30	40	0.63	1.91	64.1
ND695	10	23	33	0.64	1.51	62.3
AC Domain	11	24	35	0.48	1.74	64.3
AC Intrepid	13	28	41	0.64	1.95	56.3
AC Vista	10	28	37	0.61	1.82	61.3
Laser	11	27	37	0.68	1.88	69.3
McKenzie	9	26	34	0.55	1.83	70.5
AC Barrie	12	27	39	0.60	1.74	67.5
AC Splendor	11	25	35	0.62	1.57	61.5
SE[y]	**1.4**	**2.3**	**2.5**	**0.075**	**0.29**	**5.64**

[z]Genotypes listed in increasing lodging susceptibility.

[y]Standard error of the difference between two least-square means.

Appendix 6.17. Least-square means of culm traits measured on 13 spring wheat genotypes under a recommended seeding rate and no artificial lodging at Edmonton, AB (2001).

Genotype[z]	Plant height (cm)	No. of internodes	Adventitious roots	Internode length (cm)				Internode diameter (mm)				
				1st	2nd	3rd	4th	1st	2nd - calliper	2nd - ESEM	3rd	4th
Kohika	69	5.1	0.7	2.1	5.4	9.5	14.1	2.61	3.29	3.27	3.72	3.50
C9800L-048	73	5.1	1.8	1.8	5.1	8.9	12.5	2.51	3.18	3.31	3.25	3.15
Oslo	74	5.7	2.4	2.1	3.9	6.4	11.0	2.20	2.90	2.85	3.26	3.23
Sapphire	76	4.7	2.7	2.7	7.1	9.9	11.4	3.12	3.58	3.95	3.77	2.81
AC Foremost	71	5.5	1.4	1.8	5.4	8.3	13.0	2.47	3.40	3.47	3.70	3.67
ND695	84	5.1	1.7	2.8	7.2	13.0	15.7	2.62	3.31	3.44	3.76	3.28
AC Domain	96	5.5	0.9	2.6	6.7	12.0	18.2	2.22	2.92	3.11	3.19	3.25
AC Intrepid	95	5.1	1.3	2.9	7.2	15.2	18.2	2.61	3.41	3.01	3.58	3.09
AC Vista	80	5.3	1.5	2.3	6.1	9.6	14.6	2.50	3.16	3.23	3.42	3.35
Laser	93	5.5	2.1	2.3	4.9	9.6	16.5	2.52	3.29	3.17	3.81	4.04
McKenzie	94	5.0	1.6	3.1	9.3	15.1	19.2	2.82	3.56	3.34	3.60	3.09
AC Barrie	95	5.2	2.5	2.6	9.3	15.2	19.8	2.78	3.54	3.31	3.66	3.59
AC Splendor	98	5.5	2.7	2.2	5.8	11.9	20.3	2.52	3.26	3.04	3.67	3.60
SE[y]	**3.3**	**3.7**	**0.69**	**0.38**	**0.90**	**1.37**	**2.34**	**0.31**	**0.20**	**0.17**	**0.17**	**0.41**

Appendix 6.17. Continued.....

Genotype[z]	No. of vascular bundles			Culm wall thickness (mm)	Lumen diameter (mm)	Sclerenchyma ring thickness (μm)
	Sclerenchyma	Parenchyma	Total			
Kohika	14	29	42	0.76	1.75	80.0
C9800L-048	11	31	43	0.81	1.68	77.7
Oslo	9	27	37	0.83	1.18	93.3
Sapphire	13	35	48	0.73	2.48	74.0
AC Foremost	11	34	45	0.75	1.97	80.2
ND695	13	27	40	0.70	2.03	72.1
AC Domain	12	29	41	0.67	1.77	69.5
AC Intrepid	11	28	39	0.84	1.33	78.1
AC Vista	11	33	44	0.67	1.89	62.2
Laser	9	29	38	0.87	1.43	83.9
McKenzie	9	28	38	0.65	2.04	72.2
AC Barrie	10	32	42	0.78	1.76	78.4
AC Splendor	14	29	43	0.83	1.38	92.8
SE[y]	**0.9**	**1.9**	**2.1**	**0.065**	**0.20**	**10.08**

[z]Genotypes listed in increasing lodging susceptibility.
[y]Standard error of the difference between two least-square means.

Appendix 6.18. Poster presented at Canadian Society of Agronomy Annual Meeting in Saskatoon, July 14-17, 2002.

Assessing Lodging Resistance in Spring Wheat

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Lodging in wheat (*Triticum aestivum* L.) has typically not been a serious problem in Canada. However, with increased yields of new varieties, crop lodging may occur more often. To date, breeders have not been specifically testing for lodging resistance, rather relying on natural selection within field trials to identify those lines resistant to lodging. Unfortunately, the selection pressure within any trait is unreliable, as the environmental conditions that induce lodging are extremely variable. Due to the complexity of screening for this trait, selection for superior lodging resistant lines has been difficult.

We evaluated a number of techniques to determine whether lodging resistant lines could be easily identified in the field. We were also interested in the impact of lodging on yield in a wide range of germplasm.

Methods

We conducted this experiment over two years at the Edmonton Research Station. The trial was a four block split plot design, with wheat lines as main plots and lodging treatments as subplots. Twenty-seven wheat lines were included, representing a variety of origins, quality classes and plant architectures. The four experimental treatments included:

- Recommended seeding rate (control) - 250 seeds m^{-2}
- Doubled recommended seeding rate - 500 seeds m^{-2}
- Artificial lodging, specific application according to growth stage (ARTS)
- Artificial lodging, once-over application to entire experiment (ARTO)

Dragging a plywood apparatus lengthwise across the plot artificially induced lodging (Figure 1). The ARTS treatment, seeded at recommended rate, was applied according to a specific growth stage (Zadoks 73, early milk stage) of each wheat line, 14 days post heading. The ARTO treatment, also seeded at the recommended rate, included the artificial lodging of all 27 lines on the same day, calculated according to the mean heading date of the experiment, plus 14 days. In both years, a 10-day spread was recorded for all heading dates, creating a range of growth stages in which lodging was applied. Lodging was scored on a scale of 1 to 9, with 9 representing a completely lodged plot.

Figure 1: Apparatus used to artificially lodge a plot

Discussion

Treatments differed ($P < 0.01$) in both study years (Table 1). Lodging scores were low for all 27 lines when no artificial lodging treatments were applied (even at double seeding rates in 2001). Heavy rains and wind in mid July 2000 caused lodging in some double seeded plots. Such lodging scores were not consistent among lines in this year.

The two artificially lodged treatments were statistically different (Table 1). However, the trends of lodging resistance among lines did not differ between these two treatments. We therefore consider the once-over lodging (ARTO) treatment a more practical screening procedure for determining lodging susceptibility or resistance among wheat lines.

A wide range of responses to artificial lodging was found among the lines screened, with the same trends seen over both years (Table 2). Low scoring cultivars either had the ability to resist lodging immediately preceding the artificial lodging treatment or had the ability to recover from the lodging treatment over time. Taller lines lodged more than shorter lines, with correlation coefficients between plant height and final lodging of $r = 0.84$ (2000) and $r = 0.78$(2001).

The ability of a particular line to resist lodging under the artificial treatment resulted in minimal yield loss when compared with the untreated control of a recommended seeding rate (Figure 2). Yield was negatively correlated with lodging ($r = -0.81$ (2000)and $r = -0.75$ (2001)). As one example: under artificial lodging, Kohlka (a short statured lodging resistant New Zealand bread wheat) yielded 94% of its control. Conversely, artificially lodged AC Barrie (a tall statured Canadian Hard Red Spring Wheat) yielded 61% of its untreated control.

Table 1: Lodging scores at harvest of two seeding rates and two artificial lodging treatments for 27 spring wheat lines in 2000 and 2001.

Treatment	Year 2000	2001
No Artificial Lodging		
Recommended Seeding Rate	1	2
Doubled Seeding Rate	2	2
Artificial Lodging		
Specific Application (ARTS)	6	7
Once-over Application (ARTO)	6	6
LSD (α = 0.05)	0.4	0.7

Lodging scale 1-9, with 1 = no lodging

Table 2: Lodging scores at harvest of 10 artificially lodged varieties, presented in order of decreasing lodging resistance, along with associated plant height.

Variety	Year 2000	2001	Height[1]
AC Barrie	8	9	92
AC Splendor	7	9	92
Laser	7	8	90
McKenzie	7	9	91
AC Intrepid	6	7	93
AC Vista	6	8	85
AC Domain	4	8	91
AC Foremost	3	5	74
Oslo	2	5	83
Kohlka	1	2	73
LSD (α = 0.05)	1.3	0.8	

Lodging scale 1-9, with 1 = no lodging

[1] Referenced plant heights derived from Varieties of Cereal and Oilseed Crops for Alberta - 2002. Alberta Agriculture, Food and Rural Development. Agdex 100/32.

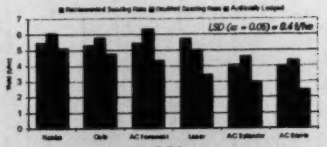

Figure 2: Grain yield of six selected spring wheat varieties either planted at recommended or double recommended seeding rate, or artificially lodged at mean heading date plus 14 days.

Conclusions

- We did not observe consistent genotypic differences in lodging in the absence of artificial lodging
- Varietal differences are consistent when artificial lodging is applied
- Bread wheat varieties are among the least tolerant to artificial lodging
- Increased lodging directly decreases yield
- A once-over artificial lodging (ARTO) treatment is an efficient and practical method of testing lodging resistance among wheat lines
- We identified genotypes resistant to artificial lodging and these lines will be incorporated into wheat breeding germplasm in Western Canada

Acknowledgments

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Appendix 6.19. Poster presented at Canadian Society of Agronomy Annual Meeting in Montreal, August 10-13, 2003.

The association of culm anatomy with lodging susceptibility in spring wheat

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Introduction

Increasing genetic lodging resistance in Canadian hard red spring wheat (CWRS) (*Triticum aestivum* L.) is an important breeding objective, particularly in high yielding environments. Lodging can result in significant economic losses from reduced grain yield and quality, and decreased harvest efficiency. However, selection for superior lodging resistant lines is difficult due to the complexity of screening for this trait under natural field conditions.

Our objectives were to determine whether lodging tolerant and susceptible genotypes differ in culm anatomy and whether any such differences are associated with lodging. Identification of traits strongly correlated with lodging may allow for the selection of lodging resistant cultivars in early generations of a breeding program.

Methods

We evaluated 13 wheat genotypes, ranging in origin, quality class and plant architecture, for their susceptibility to lodge in a field experiment conducted over two years at Edmonton, AB. Lodging was artificially induced at the early milk stage by dragging a weighted, plywood apparatus on wheels lengthwise across a plot. Plots were scored on a scale of 1 to 9 to determine lodging susceptibility of each genotype.

Two weeks prior to harvest (hard dough), five plants were randomly sampled from control plots (no artificial lodging applied). Measurements of plant height and length of each internode were recorded from the main culm of each plant. Following main culm measurements, the 2nd basal internode was excised and free hand sections were made as thin as possible from the middle of the internode. Using an environmental scanning electron microscope (ESEM) at 26x magnification and accompanying ESEM software, the following measurements were taken: culm diameter, culm wall thickness, lumen diameter, sclerenchyma ring thickness, and number of vascular bundles.

Presented data is combined over 2 years. Standard error of the difference between two least-square means (SE_{sd}) are presented throughout. Spearman rank correlations were computed on yearly least square means. A subset of 9 of 13 cultivars is reported for clarity of presentation.

Acknowledgments

This work is supported by NSERC and the Western Grain Research Foundation producer checkoff funds.

Results

Cultivars differed ($P < 0.05$) for artificially induced lodging scores and plant height (Table 1). Cultivars that were able to resist or recover from artificially induced lodging were less than 81 cm tall and cultivars that exhibited low levels of tolerance or recovery to artificially induced lodging (scoring 7 or 8) were taller than 100 cm, on average.

Basal internode length differed ($P < 0.05$) among cultivars (Figure 1). Kohika and Oslo consistently exhibited the shortest basal internodes, while McKenzie and AC Barrie consistently exhibited longer basal internodes.

Cultivars differed ($P < 0.05$) for culm diameter, culm wall thickness, and number of vascular bundles (Table 2), but not for lumen diameter or sclerenchyma ring thickness (data not shown). Lodging tolerant cultivars Oslo and Sapphire had thick culm walls, while moderately tolerant (AC Domain) and susceptible (McKenzie) cultivars had thin culm walls (Figure 2).

Plant height and the length of the 4th internode were correlated with artificially induced lodging on a genotypic basis ($r = 0.51$ for both). No other correlations were biologically significant.

Table 1. Artificially induced lodging scores and plant height of 9 wheat genotypes grown in Edmonton, AB (2000-2001).

Cultivar	Artificial lodging[1]	Plant height (cm)
Kohika	2	73
Oslo	2	80
Sapphire	3	81
AC Foremost	4	79
ND695	5	88
AC Domain	6	100
Laser	7	102
McKenzie	8	101
AC Barrie	8	104
SEsd	0.8	2.0

[1]Lodging scored 1 to 9, with 1 = no lodging.

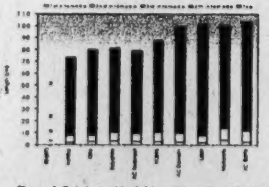

Figure 1. Total plant height and length of the four basal internodes of 9 wheat cultivars, arranged left to right in order of increasing lodging susceptibility.

Table 2. Culm diameter, culm wall thickness and number of vascular bundles of the 2nd internode of 9 wheat cultivars.

Cultivar	Culm diameter (mm)	Culm wall thickness (mm)	No. of vascular bundles
Kohika	3.15	0.72	41
Oslo	3.02	0.79	37
Sapphire	3.73	0.76	41
AC Foremost	3.32	0.69	42
ND695	3.11	0.67	36
AC Domain	2.93	0.58	38
Laser	3.21	0.78	38
McKenzie	3.13	0.60	36
AC Barrie	3.12	0.69	41
SEsd	0.164	0.045	1.8

Cultivars listed in order of increasing lodging susceptibility

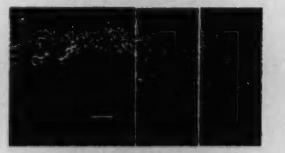

Figure 2. Differences in culm wall thickness, shown from a selected portion of the 2nd internode cross section of four wheat cultivars differing in lodging susceptibility (ordered by increasing lodging tolerance from left to right). Arrows indicate the position of the sclerenchyma ring, just below the epidermis, with a vascular bundle embedded within.

Conclusions

- Cultivars that scored low for lodging were short; high scoring cultivars were tall.
- Short, wide basal internodes with thick culm walls and a high number of vascular bundles were characteristic of some lodging tolerant cultivars.
- Although specific associations between culm anatomy and lodging scores were apparent, generally applicable associations were not observed for most traits in the 13 breeding lines studied.
- The most practical and easily selectable trait for lodging susceptibility within a wheat breeding program is plant height.